MAY 1958
LIBRARY
POFI
FISH & WILDLIFE
SERVICE

PERIODICAL
Marine Biol.
Assoc. of
the U.K.
Journal.
V.23
1938

Volume & DATE OF MAGAZINE	BORROWER'S NAME	TIME out

PERIODICAL

Marine Biol. Assoc. of
the U.K.
Journal.

V.23
1938

LIBRARY
BUR. OF COMM. FISH.
HON. BIOL. LAB.

2110^60

OBSERVATIONS ON BRITISH AND NORWEGIAN HYDROIDS AND THEIR MEDUSAE

By W. J. Rees, M.Sc.

Research Assistant at the Plymouth Laboratory

(Text-figs. 1–12)

CONTENTS

PAGE
Introduction 1
Bougainvillia muscoides (M. Sars 1846) 2
Systematic Discussion on *Perigonimus* 5
The Genus *Rhizorhagium* M. Sars 1877 6
  Rhizorhagium roseum M. Sars 1877 8
  Rhizorhagium sarsii (Bonnevie 1898) 9
  Rhizorhagium album n.sp. 9
The Genus *Leuckartiara* Hartlaub 1914 11
  The Hydroid of *Leuckartiara octona* (Fleming 1823) 12
  Leuckartiara abyssi (G. O. Sars 1873) 19
Thamnostoma russelli n.sp. 22
The Hydroid of *Euphysa aurata* Forbes 1848 25
Campanulina paracuminata n.sp. 33
Notes on other Hydromedusae 37
  Boreohydra simplex Westblad 1937 37
  Stauridium productum Wright 1858 37
  Staurocoryne filiformis Rees 1936 38
Summary 39
References 39

INTRODUCTION

This paper contains observations on British and Norwegian Hydromedusae made at Plymouth and Bergen respectively. Observations on *Campanulina paracuminata* n.sp., *Rhizorhagium album* n.sp., *Staurocoryne filiformis* Rees 1936 and on the hydroid of *Leuckartiara octona* (Fleming) were made at Plymouth during 1936 and 1937. The observations on the Norwegian forms are some of the results of a six weeks' stay at the Bergens Museum Biological Station at Herdla near Bergen.

The main object of my visit to Herdla was to work out the life history of *Perigonimus muscoides* M. Sars 1846. In addition to this life history, observations were made on several other interesting hydroids and medusae, of which the following species are described in this paper: *Leuckartiara abyssi* (G. O. Sars 1873), *Rhizorhagium roseum* M. Sars 1877, *Thamnostoma russelli*

SEP 1954
LIBRARY
POFI
FISH & WILDLIFE
SERVICE

n.sp., *Corymorpha annulicornis* M. Sars 1859. Notes are included on *Stauridium productum* Wright 1858, and *Boreohydra simplex* Westblad 1937.

I am indebted to the Challenger Society for a grant to cover my expenses at Bergen. I also wish to express my thanks to the following: to Professor August Brinkmann, Director of the Biological Station at Herdla, who gave me every facility to pursue my work; to Amanuensis D. Rustad for much help in collecting material and in setting up special apparatus; to Dr Jöran Hult (Uppsala) for the use of his "sledge dredge" at Herdla and for material from Northern Norway. My thanks are also due to Mr F. S. Russell for helpful criticism at all times.

Bougainvillia muscoides (M. Sars 1846)

Synonym: *Perigonimus muscoides* M. Sars 1846.

This species was first described by Michael Sars (1846) as *Perigonimus muscoides*. He found it growing on the test of *Ascidia mentula* Linn. and on the tubes of *Tubularia indivisa* from depths between 20 and 30 fathoms in the Mangerfjord. It has since been found by a number of investigators from Scandinavian seas and the hydroid is accurately figured by Jäderholm (1909). Stechow (1923) has described a closely related species from the Mediterranean under this name. A careful comparison of the descriptions of this hydroid and those of better known so-called "*Perigonimus*" hydroids convinced Stechow that the latter were not cogeneric with the genotype, *P. muscoides*. Rees & Russell (1937) accepted Stechow's revision in part and accordingly removed certain species from *Perigonimus*. Further revision of the British species was impossible without knowing for certain what the medusa of *P. muscoides* was, and it was this which prompted me to go to Bergen to search for it.

During my stay at Bergen numerous colonies of this hydroid were found and its medusa proved to be a *Bougainvillia*. *Perigonimus* therefore becomes a synonym of *Bougainvillia*, and the species must henceforth be called *B. muscoides* (M. Sars 1846).

B. muscoides was found on the first day of my stay at Herdla. It was taken at Bognøstrømmen in the Mangerfjord living on the test of *Ascidia mentula* Linn. dredged from depths between 10 and 80 m. It was in this fjord that Sars originally found the species growing on *Ascidia mentula* and on the tubes of *Tubularia indivisa*.

Below are given my records of this hydroid:

2. viii. 37. Bognøstrømmen, Mangerfjord. Four colonies, on four out of five specimens of *Ascidia mentula* dredged between 10 and 80 m. One colony had medusa buds and a few medusae were liberated in the laboratory on the same day.

6. viii. 37. South of North Bratholmen, Hjeltefjord, *ca.* 100 m. One small poorly developed colony, with a few medusa buds, growing on *Sertularella gayi*.

19. viii. 37. Bognøstrømmen, Mangerfjord, 40–50 m. A large well-developed colony, with numerous medusa buds, growing over the stems of *Tubularia indivisa*. A colony of *Rhizorhagium roseum* M. Sars was growing over both hydroids.

THE HYDROID. The colonies consist of upright rhizocaulome formations arising at intervals from a network of stolons running over the test of the ascidian or over the tubes of the *Tubularia*. The appearance of the colonies is quite distinct from other Norwegian hydroids. The upright branches are thicker and less branched, and the secondary branches are shorter and fewer than in young stages of other *Bougainvillia* hydroids. Sars gives an excellent coloured figure of the living hydroid and Jäderholm (1909) gives a good figure of the rhizocaulome formation.

The stems reach a height of 2 cm. and are covered by a chitinous perisarc. When the colony is young only the central tube is present. This thickens in diameter with age, and stolons from the base creep up along it on all sides so that there may be four to seven auxiliary tubes in addition to the main stem. A thick polysiphonous rhizocaulome is thus formed (Fig. 1 *a*). A similar condition has been described by Browne (1907) in *Bimeria biscayana*.

The central tube is 0·25–0·3 mm. in diameter and the auxiliary tubes are 0·1 mm. Both can give rise to hydranths. The polyps are somewhat irregularly distributed; they may occur terminally, at the ends of branches or laterally on short stems; sessile polyps also occur on the rhizocaulome itself. The hydranths are typical of *Bougainvillia*, with a prominent conical hypostome and a whorl of filiform tentacles. The terminal hydranths are usually the largest, 0·5–1·0 mm. in length and 0·2–0·3 mm. in diameter. The lateral hydranths (Fig. 1 *a*) are smaller and have eight to eleven tentacles, a feature also noted by Sars (1846). Unless the colony was very old the terminal hydranth originated from the central tube. In some of the oldest colonies seen, however, the coenosarc of the central tube had disappeared and a new terminal hydranth had developed from an auxiliary tube.

The perisarc of a stem supporting a hydranth may be slightly wrinkled and enlarges a little distally to form a slight cup into which the posterior third of the hydranth can contract. The coenosarc narrows gradually below this point to form a thin tube. The smallest hydranths, which are almost sessile on the rhizocaulome, arise from the sides of the central and auxiliary tubes. Their stalks are usually thin and have about the same diameter as the auxiliary tubes. These hydranths appear to be young ones in which the stalk later becomes much thicker and longer.

The most remarkable feature of this hydroid is the great number of medusa buds. These arise directly from the rhizocaulome and its branches (Fig. 1 *a*). They are frequently situated in rows on the auxiliary tubes and are almost sessile, having only very short stalks. A fruiting colony with its reddish polyps and the red and white medusa buds is a beautiful object when seen under a low-power lens. The largest buds are 0·4 mm. long by 0·3 mm. in diameter. When the medusa bud is almost fully developed the reddish manubrium and the brownish bulbs of the four tentacles show clearly through the thin hyaline perisarc which protects the bud. The last structures to develop in the bud are the four single oral tentacles on the manubrium. Sars' original colony had medusa buds, but these were not quite fully developed, and the bud which he pressed out of its envelope (Sars, 1846, tab. 1, fig. 21) showed the manubrium and the four marginal tentacles, but not the four oral tentacles.

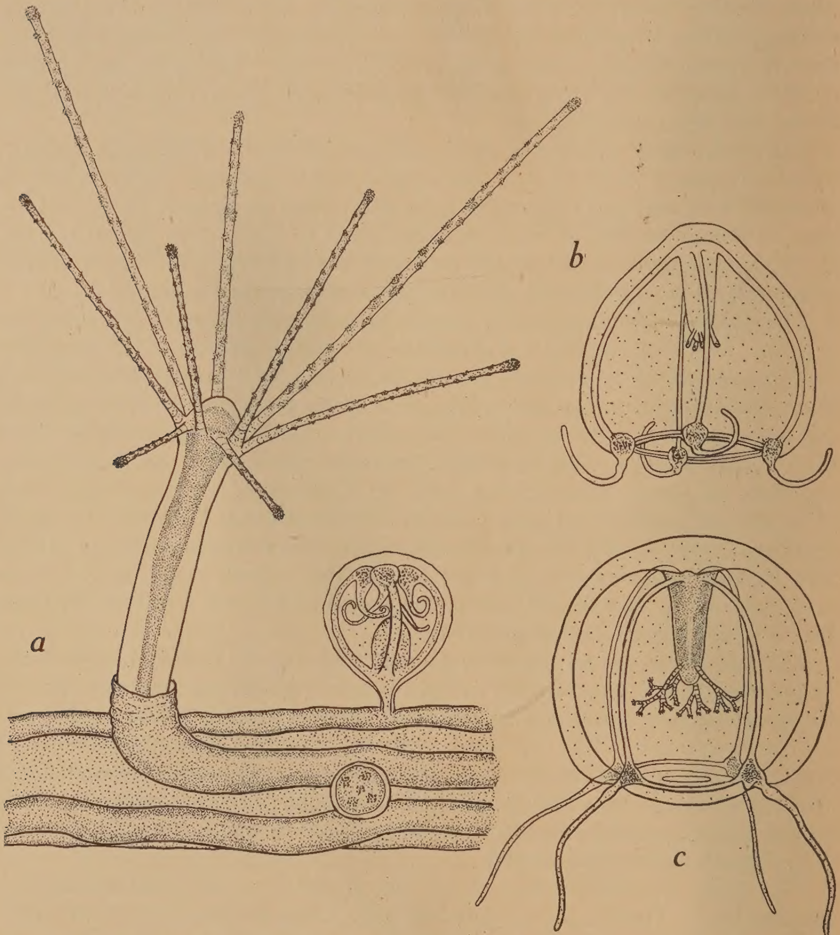


Fig. 1 *a–c*. *Bougainvillia muscoides* M. Sars: *a*, portion of the rhizocaulome bearing a lateral hydranth and two medusa buds, Herdla, 7. viii. 37; *b*, newly liberated medusa, Herdla, 3. viii. 37; *c*, young medusa obtained from the plankton in the Hjeltefjord, 30. viii. 37.

Allman (1863) was thus led to believe that the medusae were of a similar type to those of *Atractylis repens* (Wright, 1857) and accordingly placed this and other similar species in *Perigonimus*. Later authors, with the exception of Stechow (1923) and Rees & Russell (1937), have followed Allman and have referred this species to the Pandeidae (Tiaridae).

The newly liberated medusa (Fig. 1 *b*) is bell-shaped, as high as wide, with a diameter of 0·55–0·65 mm. The jelly is thin, but thicker nearer the apex than elsewhere, and there are numerous scattered nematocysts on the exumbrella. The velum is well developed. The stomach is short and conical, barely reaching to half the height of the subumbrellar cavity. Four unbranched oral tentacles, 0·07 mm. in length, with a few terminal nematocysts, arise above the mouth margin. The four radial canals and ring canal are narrow. There are four well-developed perradial bulbs, each with a single tentacle. There is a slight swelling at the base of each tentacle just before it joins the bulb, and this appears to be characteristic of this medusa. There are no ocelli. The reddish colour of the manubrium, so conspicuous in the bud, is less brilliant in the newly liberated medusa, but the reddish brown pigment in the tentacle bulbs is quite distinct. The oral tentacles of one medusa kept for a few days in the laboratory were beginning to branch. This medusa measured 0·85 × 0·8 mm.

I obtained a young medusa (Fig. 1 *c*) from plankton from the Hjeltefjord on August 30 1937. This was in a later stage of development than those I had been able to rear. The medusa was immature and measured 1·55 mm. high and 1·65 mm. in diameter. The oral tentacles on the manubrium were twice dichotomously branched. On each marginal bulb there was a rudiment of a second tentacle developing on the right side of the existing one. Each marginal tentacle possessed the characteristic swelling at its base near the bulb. There were no ocelli. The colour of the manubrium varied from reddish orange to red, and the tentacle bulbs were yellowish brown.

The medusa was identified as *Bougainvillia nordgaardi* (Browne). Kramp & Damas (1925) have described various stages in the development of this medusa. My medusa from the plankton corresponds to their Stage 2. The stage which Kramp & Damas call Stage 1 is a medusa several days old in which the oral tentacles have become branched. Their medusa appears to have lost its four tentacles.

The similarity between the medusa taken from the plankton and those reared from the hydroid points to the extreme probability that the medusa of *B. muscoides* is *B. nordgaardi* (Browne).

Systematic Discussion on *Perigonimus*

The discovery that the medusa of *Perigonimus muscoides* is a *Bougainvillia* is of considerable importance in the classification of those species which have up to now been referred to the genus *Perigonimus*. It necessitates the revision of all so-called "*Perigonimus*" hydroids because *Bougainvillia muscoides* was the genotype of *Perigonimus*.

Since *Bougainvillia* is the older generic name, *Perigonimus* becomes its synonym and the latter name can no longer be used for those species of "*Perigonimus*" whose medusae are not Bougainvillids. Stechow (1923) expressed the opinion that *P. muscoides* was not cogeneric with the other species of "*Perigonimus*" then referred to the genus, and accordingly restricted the name *Perigonimus* to this species and included provisionally also *Bimeria biscayana* Browne 1907. He proposed the use of the medusa name *Leuckartiara* Hartlaub 1914 for the hydroids producing medusae with two opposite tentacles. Two of these species have since been removed to the genus *Amphinema* Péron & Lesueur 1809 by Rees & Russell (1937). The advisability of using the generic name *Leuckartiara* will be discussed under the account of this genus.

Any revision of the genus *Perigonimus* in its widest sense must also include the genera *Atractylis* Wright 1858, *Wrightia* Allman 1872, *Dinema* van Beneden 1866, *Rhizorhagium* M. Sars 1877, *Gravelya* Totton 1930, and to a certain extent *Bougainvillia* Lesson 1836. It is necessary to clarify the position of these forms with fixed gonophores at present referred to some of these genera.

The differences between the trophosomes of *Bougainvillia* and *Leuckartiara* are very slight. Usually the *Bougainvillia* hydroid is more branched, but there are exceptions, and the presence of a dilatation of the perisarc around the base of the hydranth in many species of *Bougainvillia* makes them very difficult, if not at present impossible, to distinguish from *Leuckartiara*. However, their medusae belong to the Bougainvilliidae and the Pandeidae. To which of these families are we to refer the non-medusa-bearing forms? Our knowledge of many of these is very incomplete at the present, and it would be inadvisable to put them into either *Leuckartiara* or *Bougainvillia*. The only alternative is to put them into a genus of their own until their exact systematic position can be ascertained.

There are several generic names which come under consideration. Allman (1872) restricted the genus *Atractylis* Wright 1857 to *A. arenosa* Alder (1862), which has fixed gonophores. Later he discarded *Atractylis* because it was preoccupied by a plant of that name. In its place he erected his genus *Wrightia*, although he knew it was preoccupied by *Wrightia* Agassiz (1862), a genus synonymous with *Campanulina* van Beneden which had priority over it. Totton (1930) has selected *Atractylis ramosum* (= *Bougainvillia ramosum*) as the genotype of *Atractylis*, so that this genus is now sunk under *Bougainvillia* Lesson.

The oldest valid* generic name is *Rhizorhagium* M. Sars 1877, and this genus is discussed further below.

THE GENUS *RHIZORHAGIUM* M. SARS 1877

Synonyms: *Wrightia* E. S. Russell 1907.
Gravelya Totton 1930.

The genus *Rhizorhagium* was erected by Sars (1877) for a Norwegian species which he called *R. roseum*. He laid particular stress on the fixed nature of the gonophores as the chief character of his genus. Bonnevie (1898) described a new species, *Perigonimus sarsii*, which together with *Rhizorhagium roseum* she referred to the genus *Perigonimus*. Stechow (1923) referred the above, together with *Perigonimus antarcticus* Hickson & Gravely 1907 and *Atractylis coccineus* Wright (see Russell, 1907), to *Rhizorhagium*.

---

* *Dinema* van Beneden 1866 is preoccupied by *Dinema* Fairmaire 1849, an insect genus.

The last of these, as will be shown later, is in all probability identical with *R. roseum* Sars. For reasons already given (see p. 6) these species hitherto referred by some authors to "*Perigonimus*" must be kept separate from *Bougainvillia* and *Leuckartiara* until later work with living material reveals their exact systematic position.

Levinsen (1892) described *Rhizorhagium roseum* from Greenland as *Garveia groenlandica* (Broch, 1916). This raises the question whether all the above species should not be included in the genus *Garveia* Wright 1859. The chief characters of *Garveia* as defined by Allman (1872) were the well-developed branching hydrocaulus, the fusiform hydranth with a whorl of filiform tentacles around a conical proboscis, and reproduction by means of fixed gonophores borne on short stalks. Torrey (1902) united *Garveia* with *Bimeria* Wright 1859, a step which I cannot but regard as retrogressive (see p. 25). He referred *Perigonimus formosus* Fewkes, an unbranched form closely resembling *Rhizorhagium roseum*, to his genus "*Bimeria*".

The creeping hydrorhiza with the simple unbranched stems each bearing a single hydranth is characteristic of all these species with fixed gonophores previously referred to *Perigonimus*, and I feel hesitant in referring them to a genus such as *Garveia* where the hydrocaulus is typically a well-developed branched tree-like growth. For the present therefore it appears best to retain *Rhizorhagium* for the following species: *R. roseum*, *Perigonimus sarsii*, *P. antarcticus*, *P. formosus* Fewkes and a new species *Rhizorhagium album* to be described later.

The genus *Gravelya* was founded by Totton (1930) for *Perigonimus antarcticus* and was defined as follows: "Monoecious *Bougainvillidae* with numerous dimorphic cryptomedusoid gonophores scattered over the hydrorhiza." His genus clearly falls into the synonymy of *Rhizorhagium*. No stress can be laid on the word "Bougainvillidae" in his definition because the trophosome is distinctly like that of the hydroid of *Amphinema dinema*. Neither can the degree of development of the gonophore be stressed as a generic character; it is more suitable as a specific one.

The genus may be defined as follows:

Polyp stems, simple, unbranched and arising either from a creeping anastomosing hydrorhiza or from a weakly developed rhizocaulome formation; polyps clavate or fusiform with a single whorl of filiform tentacles around the base of a conical proboscis and partially retractile into a slight dilatation of the perisarc. Gonophores fixed, borne on short stalks on the hydrorhiza or on the rhizocaulome formation.

The above diagnosis does not differ in essentials from that of Sars. The specific characters of *Rhizorhagium roseum* which were included by Sars have been omitted and the definition of the genus emended so as to include *Peri-*

gonimus sarsii Bonnevie 1898 and *Rhizorhagium album* n.sp.; *Perigonimus antarcticus* falls naturally into the genus.

Rhizorhagium roseum M. Sars 1877

Synonyms: ? *Atractylis coccineus* Wright 1861.
Perigonimus roseus Bonnevie 1898.
Atractylis coccineus Russell 1907.
Wrightia coccineus Russell 1907.
Garveia groenlandica Levinsen 1892.
Perigonimus (*Rhizorhagium*) *roseus* Broch 1928.

This species I found at Herdla on several occasions. Colonies were found growing on *Tubularia indivisa* at Rong Sund and Bognøstrømmen. One colony from Bognøstrømmen was creeping over the stems of *Bougainvillia muscoides*.

The measurements of a fruiting colony are given below:

Measurements in mm.	
Length of hydranth	0·4 –0·45
Diameter of hydranth	0·3 –0·35
Length of hydrocaulus	3·0 –3·5
Diameter of hydrocaulus	0·12–0·2
Length of gonophore	0·9 –1·2
Diameter of gonophore	0·5 –0·75
Length of gonophore stalk	0·35–0·7

According to Broch (1916) the stalks may reach a length of 12 mm. in larger colonies. The tentacles vary from six to twelve in number. The whole colony when alive had a rosy colour. Sars (1877) and Jäderholm (1909) give excellent figures of this hydroid.

I can find no fundamental difference between the descriptions of the *Atractylis coccineus* described by Russell (1907) and *Rhizorhagium roseum*. Sars (1877) states that the gonophore is naked, while that of Russell's species is covered by a thin perisarc. A close examination of living material at Herdla revealed the presence of this thin perisarc. Broch (1916) also found a perisarc covering the gonophore, and states that it flays off when the gonophore is fully grown. The hydranth in *Atractylis coccineus* Russell is nearly always bent at an obtuse angle with the stalk, and the same characteristic has been figured for *Rhizorhagium roseum* by Sars & Jäderholm. It was also characteristic of all my colonies from Herdla. The habitat, the colour, the wrinkling of the perisarc, and the short-stalked gonophore are alike in both, and there seems little doubt that they are identical.

Whether this species is the same as the original *Atractylis coccineus* described by Wright (1861) is impossible to tell because the original description lacked a figure and no gonophores were found. It is therefore noted as a doubtful synonym of *Rhizorhagium roseum*.

The species is very common around the Norwegian coast and has been found in the White Sea and Novaya Zembla (Schydlowsky, 1901). It was first recorded from Greenland by Levinsen (1893) as *Garveia groenlandica*. A re-examination of the original specimen by Broch (1916) showed that the specimen in question should have been referred to *Rhizorhagium roseum*. Jäderholm (1909) has given an excellent figure and a list of Swedish records. There are numerous records from east and west Greenland (see Kramp, 1914, 1932 *a*, *b*). According to Fraser (1937) it is found on the Pacific coast of North America. To these we must add Russell's record from Millport on the west Scottish coast.

Rhizorhagium sarsii (Bonnevie 1898)

Synonym: *Perigonimus sarsii* Bonnevie.

This hydroid has only been recorded from Norway. Bonnevie found it at Christiansund, but states that it had been previously found in the Oslofjord by G. O. Sars and later by Greig at Bognøstrømmen in the Mangerfjord. It has since been found by Broch (1905), one colony on *Portunus depurator* and another on *Corystes cassivelaunus*. A redescription of this species from living material is much to be desired. Several points in Miss Bonnevie's description need amplifying and verifying. During my stay at Herdla I spent much time searching for this hydroid at Bognøstrømmen, but did not succeed in finding it. I did, however, find a colony of *Rhizorhagium roseum* growing over the stems of *Bougainvillia muscoides*. When alive the stolons of the two hydroids could easily be distinguished by their colour, but when preserved the stolons were indistinguishable. It appears possible to me that a well-developed colony of *Rhizorhagium roseum* growing over a dead colony of *Bougainvillia muscoides* could easily be mistaken for *Rhizorhagium sarsii*.

Rhizorhagium album n.sp.

A very small hydroid found by Mr F. S. Russell growing on small weeds in a rock pool at Newquay, Cornwall, has proved to be a new species. Mr Russell kindly gave me the hydroid to rear and describe. When found the hydroid appeared to be a creeping or a juvenile form of a *Bougainvillia* or a species of "*Perigonimus*". Styloid gonophores, however, were developed. The species could not be referred to any known species with certainty and has therefore been described as new. It approaches nearest to and may be identical with *Eudendrium pudicum* Van Beneden 1866. Van Beneden regarded his species as identical with *Trichydra pudica* Wright, which, however, is quite a different kind of hydroid from the one he figures. Gonophores were not observed by Van Beneden, and there is no certainty that his species is identical with mine. *Eudendrium pudicum* Van Beneden is therefore noted as a doubtful synonym. The systematic position of this species is discussed later in this paper.

Three small colonies were found on a filamentous alga. The polyps could be distinguished with the naked eye as minute white specks. The colonies were not reproducing and did not do so until they had been four months in captivity.

The stolons creep over the alga or over each other and sometimes branch (Fig. 2 *a*). They are covered by a thin transparent perisarc which is irregularly wrinkled. They are 0·1 mm. in diameter. The stems are very short, and sometimes the polyps are subsessile. The stems, like the stolons, are irregularly wrinkled and rarely exceed 0·3 mm. in length. The perisarc of the stems expands to form a close-fitting pseudohydrotheca around the base of the hydranth. How far it extends on the hydranth itself was very difficult to determine. The hydranths are tubular with a single whorl of six to ten filiform tentacles around a small but distinct hypostome (Fig. 2 *b*). The polyps vary from 0·35 to 0·55 mm. in length with a transverse diameter of 0·1–0·14 mm.

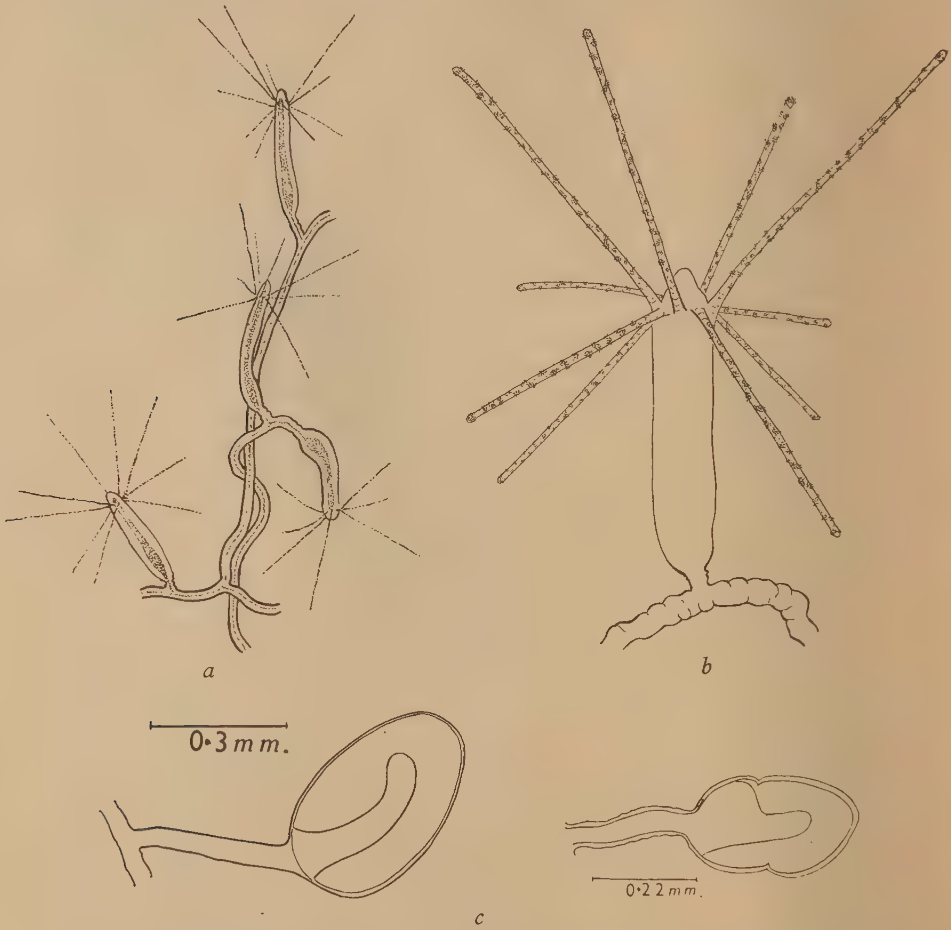


Fig. 2 *a–c*. *Rhizorhagium album* n.sp.: *a*, general appearance of a colony kept in the Plymouth Laboratory, 5. iv. 37; *b*, single hydranth, 6. iv. 37; *c*, male gonophores.

The polyps themselves are white in colour with a light brown endoderm. Gonophores were observed developing on April 3 1937. These were fully developed seven days later. Others were developed later in the year. On all three colonies only male gonophores were developed (Fig. 2 *c*). These were typical styloid gonophores borne on fairly long stalks 0·3–1·0 mm. long. The largest gonophore seen had a diameter of 0·4 mm.

This species differs in many characters from other species now placed in *Rhizorhagium*. The hydranths are almost sessile, and the gonophores stalked, as compared with the long-stalked hydranths and almost sessile gonophores in typical species of *Rhizorhagium*. Owing to the unsatisfactory state of our knowledge of the *Bougainvillia-Leuckartiara* type of hydroids I feel hesitant in erecting a new genus to take this species and provisionally therefore include it in *Rhizorhagium*.

The following is a concise definition of the new species:

Rhizorhagium album n.sp. (Fig. 2)

Synonym: ? *Eudendrium pudicum* van Beneden 1866.

Stems and stolons covered by a distinct, irregular, and sometimes faintly wrinkled perisarc. Hydranths tubular with a whorl of six to ten filiform tentacles around a bluntly conical proboscis and borne on very short hydrocauli.

Gonophores: male gonophores are styloid, borne on distinct stalks. Female gonophores unknown.

Distribution: Newquay, coast of north Cornwall.

THE GENUS *LEUCKARTIARA* HARTLAUB 1914

Hydroid Synonyms: *Atractylis* Wright 1858 (in part).
Perigonimus Allman 1863 (in part).
Dinema van Beneden 1866.

The genus *Leuckartiara* was erected by Hartlaub (1914) for three species of pandeid medusae. The hydroids of this and allied genera had been referred by Allman (1863, 1864 *b*) and later workers to the genus *Perigonimus* Sars. It has been shown earlier in this paper that *Perigonimus* can no longer be used for hydroids of this type which produce pandeid medusae. Stechow (1923) has used the name *Leuckartiara* for hydroids of this type, which produce medusae with two tentacles. Great care, however, must be taken to use this name correctly, because a great many of the so-called "*Perigonimus*" hydroids produce medusae which do not belong to the medusa genus *Leuckartiara*; for example, *Perigonimus serpens* Allman 1863 is the hydroid of *Amphinema dinema* Péron & Lesueur. Apart from the hydroids at present referred to the genus *Amphinema*, the only two hydroids, producing pandeid medusae, whose life histories are known with certainty are *Perigonimus repens* (which is the hydroid of the medusa *Leuckartiara octona*) and *Perigonimus cirratus* Hartlaub 1914, of which the medusa is *Halitholus cirratus*. Both hydroid and medusa should be called *H. cirratus*.

Those species whose newly liberated medusae with two opposite tentacles are obviously pandeid medusae should, I think, be referred provisionally to *Leuckartiara* as "*Leuckartiara*" spp. *Perigonimus nudus* Stechow 1919 obviously has no affinities with *Bougainvillia* or *Leuckartiara*. Indeed, as Stechow himself observes it is probably related either to *Campanopsis*, *Hydranthea* or to *Halecium*; it needs a new generic name.

I have provisionally included *Perigonimus abyssi* G. O. Sars 1873 in *Leuckartiara* as *L. abyssi*.

The Hydroid of Leuckartiara octona (Fleming 1823).

The hydroid of *Leuckartiara octona* (Fleming) is best known by the name *Perigonimus repens* (Wright 1857). It is one of the commonest species occurring in British waters. The species is very variable in form, and this led earlier workers to regard certain types of growth as distinct species. The various descriptions of this hydroid are very scattered in the literature, and there is no single adequate description. It is therefore considered desirable to redescribe this species and to record the variations to which it is subject under different conditions of habitat. The medusa is well described by Hartlaub (1914).

HISTORICAL. The species was originally described by Wright (1857) as *Eudendrium pusillum*. He found it growing on the back and walking legs of spider crabs and on sertularians. At the same time he described another species, *E. sessile*, which he found growing on shells from deep water in the Firth of Forth and declared that the medusae on liberation seemed to be identical. It will be shown later in this paper that *E. sessile* is the creeping form of *E. pusillum*. A year later, in 1858, Wright refers to his *E. pusillum* as *E. repens*, though he gives no reason for the change of the name. A search through the literature reveals that a species of *Halecium* was described by Sars (1857) as *Eudendrium pusillum*. Perhaps this is the reason for the change of name.

In the same paper (1858) Wright dismembers the old genus *Eudendrium* Erhenberg into *Eudendrium* proper with a trumpet proboscis and *Atractylis*. He referred his two "*Eudendrium*" species to this latter genus with *E. ramosum* (van Beneden, Dalyell) (=*Bougainvillia ramosa*) as the genotype. Allman (1863, 1864) removed Wright's two species to the genus *Perigonimus* Sars 1846, and to this genus he also referred a new species, *P. minutus*, which he found living on the operculum of *Turritella communis* Lamarck from the Shetland Islands. Opinion is divided as to whether this species is synonymous with *Perigonimus repens*. Hincks (1868) lists it as a synonym of *P. repens*, but Allman (1872) separates them again.

The species described by van Beneden (1866) as *Dinema slabberi* is undoubtedly this species.

The next important contribution to the life history is that of Hartlaub (1895) who succeeded in rearing the medusa to a stage when it could be recognized as a young pandeid (*Tiara*). He also found medusa buds developing from both the stolon and the hydrocaulus, which made him doubtful of the identity of his species. Later (1914) he refers it to *Perigonimus repens* and gives the synonymy of the species and an excellent description of the medusa for which he erected the genus *Leuckartiara*.

Broch (1916) discussed the distribution of the species and the nature of the pseudohydrotheca. Stechow (see p. 11) was the first to separate this species from *Perigonimus*. In later papers he refers to the hydroid as *Leuckartiara pusilla* (Stechow, 1929).

Records of this hydroid are very numerous, but only the more important references are given in the bibliography.

THE HYDROID. The hydroid is nearly always found living in association with other animals. It occurs chiefly on the shells of molluscs and on the legs and carapace of various crabs, but has been found growing on a number of other animals. Colonies vary greatly in their mode of growth, depending on the nature of the host and on the substratum. I propose to describe below typical colonies from the shell and operculum of *Turritella communis* Lamarck, *Scaphander lignarius* (Linn.), *Corystes cassivelaunus* (Pennant), and *Agonus cataphractus*.

Shells of living *Turritella communis* dredged from Rame mud frequently carried small colonies with almost sessile hydranths arising from a creeping reticulate stolon 0·05 mm. in diameter. The hydranths were small (Figs. 3 *a*, *b*), rarely with a height (to top of hypostome) of more than 0·5 mm. They possessed a distinct conical hypostome and a single whorl of 4–8 filiform tentacles. The close-fitting perisarc of the hydranth was thin and reached as far as the base of the tentacles. Medusa buds were borne at intervals on the creeping stolon. Like the hydranths they were also almost sessile with a very short stalk. The newly liberated medusae were typical specimens of young *Leuckartiara*; some were reared in the Laboratory until the gonads began to appear when the species could be recognized for certain as *Leuckartiara octona*.

Colonies from the opercula of living *Turritella* shells and those on the "upper sides" of shells of the same species inhabited by small hermit crabs were very similar in appearance (Figs. 3 *a*, *c*). A portion of a typical colony growing on a shell inhabited by a hermit crab is shown in Fig. 4 *a*. The stems were fairly long, smooth, sometimes ringed at the base, generally unbranched, but occasionally a single stem bore two hydranths. The total height of the stems was 1·5–2·5 mm. In this colony young and old polyps were found. The hydranths were fusiform with a loose-fitting, irregularly wrinkled perisarc, reaching as far as the base of the tentacles. The largest hydranths had a length (to top of hypostome) of 0·5 mm. and had 8–10 tentacles. The smallest hydranths had 4–8 tentacles. Medusa buds were borne on both hydrocaulus and hydrorhiza. The medusa buds had distinct stalks with a smooth or wrinkled perisarc. The stalks were never longer than the medusa buds. The "sides" and "lower side" of the shell showed transitional polyps between the sessile form and the branched form on the upper part of the shell (Fig. 4 *b*). Medusae were also reared from these colonies and they developed into typical *Leuckartiara octona* medusae.

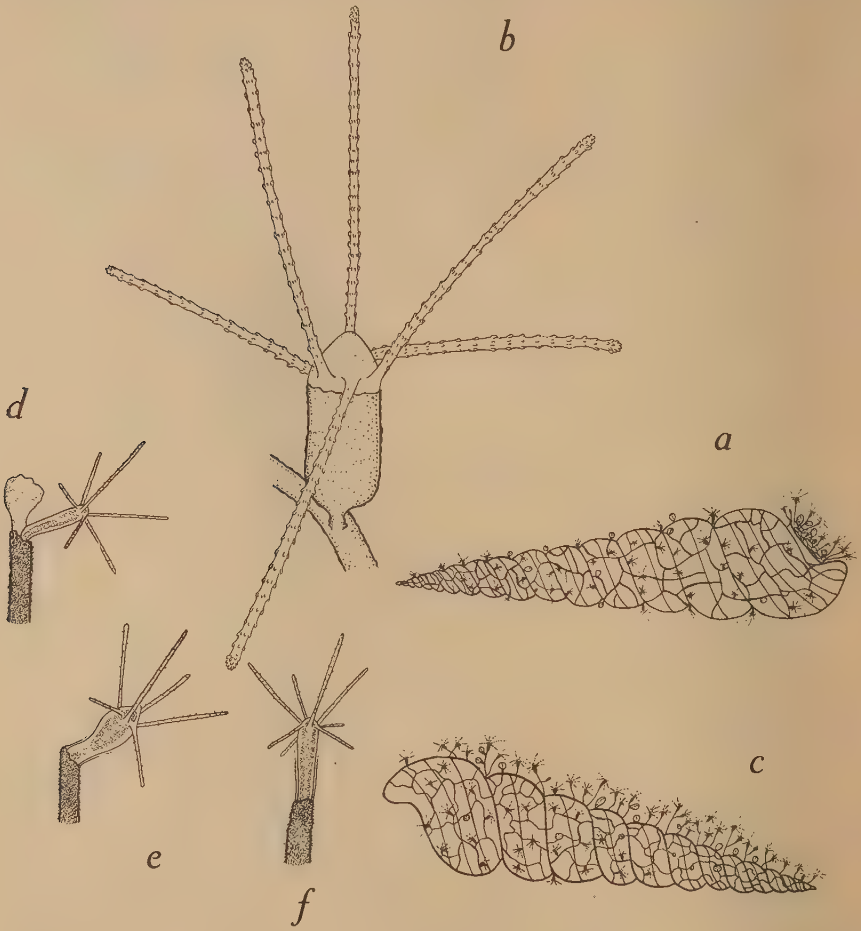


Fig. 3 *a–f*. *Leuckartiara octona*: *a*, creeping form of the hydroid on a shell of *Turritella communis* with the branched form on the operculum, 2. vii. 37; *b*, single hydranth of the creeping form on a living *Turritella* shell, 12. iii. 36; *c*, the branched form of the hydroid on the "upper side" of a shell of *Turritella* inhabited by a hermit crab, with the creeping form on the "lower side", 16. iii. 36; *d–f*, regeneration of a new hydranth from an old stem growing on *Scaphander lignarius*, 17. ii. 37; all from Plymouth.

Colonies living on the shells of *Scaphander lignarius* usually grow on the posterior part of the shell. The stolons form an open network. The stems are long, of uniform thickness and covered with a layer of fine mud particles. The stems bear one or two hydranths. The hydranths are usually small, rarely having a diameter much greater than that of the stem. The hydranths frequently die down and new ones are formed from the side of the hydrocaulus just below the position of the old hydranth (Fig. 3 *d*, *e*, *f*). Medusa buds are borne on the hydrocauli and only rarely on the stolons. A single hydrocaulus may have one to three medusa buds.

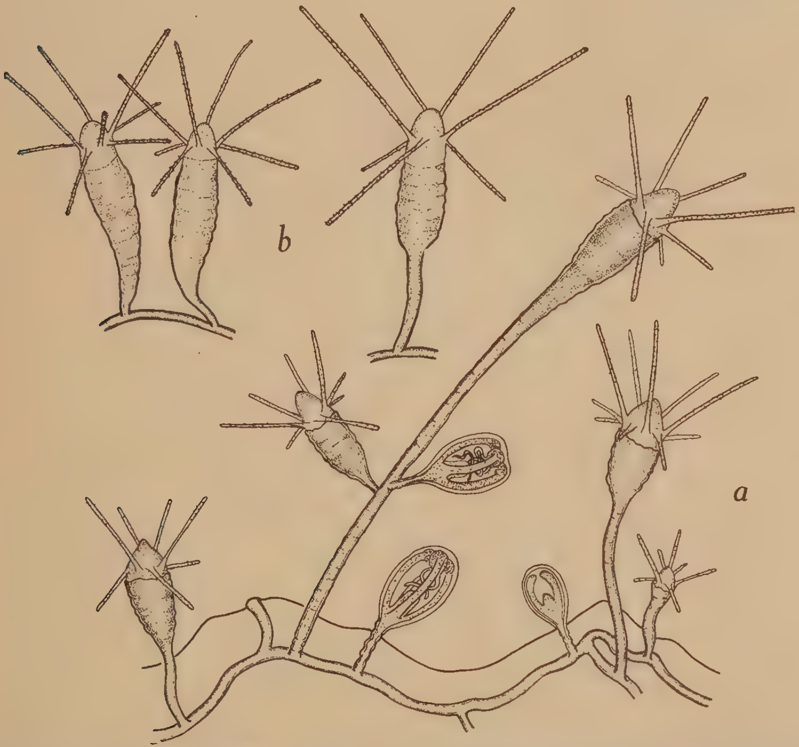


Fig. 4 *a*, *b*. *Leuckartiara octona*: *a*, hydroid colony growing on a *Turritella* shell inhabited by a hermit crab; *b*, transitional polyps on the same *Turritella* shell; Plymouth, 16. iii. 36.

Specimens of *Corystes cassivelaunus* found at Plymouth frequently carry well-developed colonies which cover the sides of the carapace, the underside and the walking legs. The following description is based on a colony caught in Cawsand Bay on June 29 1937. The hydroid had a tufted appearance, the hydranths appeared white and the stems brownish or horn coloured (Fig. 5). The stolons were 0·05–0·07 mm. in diameter and formed an open network with well-developed branched stems arising at frequent intervals from it. The stems were branched three or four times, rising to a height of 2·5–3·0 mm. At their point of origin the stems were annulated having 2–6 annulations, and at this point having a diameter of 0·06–0·08 mm. Above, the stems were slightly and irregularly wrinkled but never annulated. The perisarc widens below the hydranth to form a cup-shaped or funnel-shaped pseudohydrotheca which was much wrinkled. The pseudohydrothecae were 0·4–0·45 mm. in length and 0·21–0·3 mm. in diameter; they reached as far as the base of the tentacles. The hydranth itself was spindle-shaped with a distinct hypostome and a whorl of 8–10 tentacles held rather stiffly. Sometimes the tentacles were alternately elevated and depressed. The total length of the hydranth from the base of the pseudohydrotheca to the hypostome was 0·5–0·6 mm. The hydranths and the upper part of the stems were covered by adhering particles of mud. The pseudohydrothecae were slightly gelatinous and mud particles stuck to them very easily.

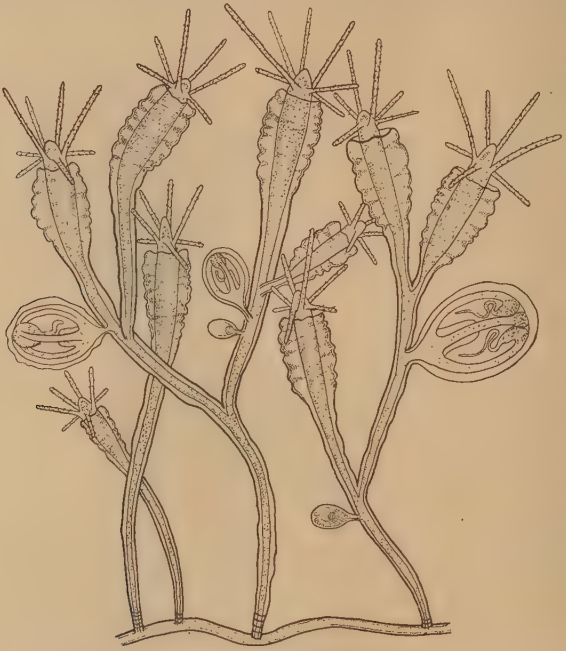


Fig. 5. *Leuckartiara octona*; well-developed colony on *Corystes cassivelaunus*; Plymouth, 29. vi. 37.

Medusa buds were borne at all levels on the hydrocauli, but very few were seen developing from the hydrorhiza. There were never more than four medusa buds on the same hydrocaulus. The stalks of the medusa buds were short, and the largest buds seen had a diameter of 0·3–0·35 mm. and a length of 0·35–0·45 mm.

Mr A. J. Smith found a colony of this hydroid growing on a fish, *Agonus cataphractus*, captured in the Cattewater, Plymouth, in February 1910. The hydroid covered portions of the back, fins and the under side of the fish with a luxuriant growth. The stems arose from a creeping network of anastomosing stolons 0·05 mm. in diameter. The stems were usually unbranched, but occasionally stems bearing two hydranths were found. The perisarc was thin, rarely ringed at the base and formed a loose sheath covering the lower part of the hydranth as far as the base of the tentacles. The hydranths were spindle-shaped with six to ten tentacles. Medusa buds were very numerous and were borne on both stems and stolons on distinct stalks with an irregularly wrinkled perisarc. The stems bore from one to four medusa buds. The table below gives measurements of fully developed hydranths and fully developed medusa buds.

Measurements in mm.

Total height (to hypostome)	3·8
Length of hydranths	0·65–0·7
Diameter of hydranths	0·25–0·3
Diameter of hydrocaulus	0·08–0·12
Length of medusa buds	0·6
Diameter of medusa buds	0·45–0·5
Length of stalk of medusa buds ...	0·1 –0·3
Diameter of stalk of medusa buds ...	0·05

In appearance this colony compares favourably with the figure of *Perigonimus pugetensis* Heath 1910, also found on a fish. Hartlaub (1914) doubted whether this species was distinct from *P. repens*.

Discussion. The great variability shown by this hydroid in its mode of growth probably depends largely on the nature of the host and on the substratum on which the host lives.

The creeping form on the shells of living *Turritella communis* may be a juvenile form, but, as the colonies have medusa buds at the right season, it is more likely that this creeping form is an adaptation to life on a shell which is nearly always buried in mud. The shell is dragged along by the snail and probably frequently rolls over so that no one surface is free from friction. The hydranths remain almost sessile because the depressions on the shell afford them some measure of protection. It was this form which Wright (1857) described as *Eudendrium sessile*.

Colonies living on the opercula of *Turritella* shells have much more protection, and they have an erect hydrocaulus which may be branched. Colonies on the "upper side" of shells of this species inhabited by hermit crabs also develop an upright branched hydrocaulus (Fig. 3 *c*). The shells inhabited by hermit crabs are much more stable, and the polyps on the "upper side" have the opportunity to grow up into branched colonies while the lower side still has the creeping form (Fig. 3 *c*). Intermediate polyps between the branched form and the creeping form are frequently found on shells of *Nassarius* *reticulatus*. The strong branched growth found on *Corystes* and other crabs will be discussed below.

The perisarc, especially the pseudohydrotheca, is subject to great variation which may possibly be influenced by the kind of food that the colony is able to obtain. Polyps of the creeping form on *Turritella* shells probably feed on micro-organisms in the mud, so that the coelenteron of each polyp is never dilated by big food masses and so remains as a close-fitting sheath on the hydranth. However, the colonies on the opercula and on the shells inhabited by hermit crabs are moved about more quickly and therefore have a better chance of gorging themselves. The polyps on the shell of the hermit crab may also catch some of the pieces of an animal caught by the hermit crab. This would cause the hydranth and its pseudohydrotheca to become considerably distended. After the digestion of the food the hydranth would shrink to its normal size leaving the perisarc as a loose-fitting sheath. A slight shrinking of the latter would result in the irregular wrinkling so typical of the pseudohydrothecae of well-developed colonies. The colonies on crabs are subject to more movement than those on shells and may receive larger particles of food from the host so that the pseudohydrothecae are largest in these colonies. The perisarc was thickest and more strongly developed in colonies from *Corystes* and other crabs. It was sometimes ringed at the base, but this character was very variable. When newly formed the perisarc was thin and transparent. The colony figured by Allman (1872) as *Perigonimus minutus* appears to me to be a young colony of this species.

In all my living specimens the pseudohydrothecae never extended beyond the base of the tentacles, but in some preserved specimens the contraction of the hydranth made it appear that the hydranth was largely retractile. *P. vestitus* Allman 1864 *b* has been regarded by Hartlaub (1914) and Kramp (1927) as synonymous with this species. Moreover, *P. vestitus* has, according to Allman's text and figure, a continuation of the perisarc beyond the base of the tentacles as a thin transparent membrane which is continued almost as far as the mouth. It must, therefore, be retained as a separate species. Stechow (1923) has placed this species in the medusa genus *Cytaeis* as *C. vestita*, although Allman's figure clearly shows that this medusa is a typical pandeid.

The position of the gonophores on the hydrocaulus and on the stolon, together with the branched and sessile hydranths in his two forms, led Wright to regard his *Eudendrium pusillum* and his *E. sessile* as two distinct species. Medusae have been reared in the Plymouth Laboratory which leaves no doubt that *E. sessile* is identical with the branched form.

The hydroid, as has already been stated, grows on a wide range of animals. Stechow (1929) found this species growing on the under side and between the parapodia of *Aphrodite aculeata*. It has not yet been recorded from this species at Plymouth.

The hydroid and medusa seem to have a cosmopolitan distribution. The hydroid has been recorded from Arctic seas by Kramp (1938), from the Pacific coast of North America by Calkins (1899), Torrey (1902) and Fraser (1937), from South America by Stechow (1919) and from the Indian Ocean by Leloup (1932), to mention only a few of the records.

The synonyms of the hydroid are given below:

Leuckartiara octona (Flemming, 1823)

Hydroid synonyms: *Eudendrium pusillum* Wright 1857; *E. sessile* Wright 1857; *E. repens* Wright 1858; *Atractylis repens* Wright 1858; *A. sessilis* Wright 1858; *Perigonimus minutus* Allman 1863; *P. sessilis* Allman 1864; *P. pusillus* Allman 1864; *Dinema slabberi* van Beneden 1866; ? *Perigonimus pugetensis* Heath 1910; *Leuckartiara pusilla* Stechow 1929.

Leuckartiara abyssi (G. O. Sars, 1873)

Synonym: *Perigonimus abyssi* G. O. Sars.

This small species was found living on the shells of *Nucula timidula* at Herdla. It was originally described by G. O. Sars (1873) from Hitvingsø, growing on shells of living *Dentalium* at depths varying from 80 to 200 fathoms, and also on shells of *Nucula timidula* from the Hardangerfjord down to 400 fathoms. Since then there have been numerous records from Scandinavian seas (for details see Jäderholm, 1909; Ritchie, 1913; and Broch, 1916). It has also been reported from Greenland by Kramp (1911), as *Perigonimus* sp. by Broch (1916), and from Spitzbergen by Broch (1909) from very shallow water. The only British record is that of Ritchie (1913), who records it from the Atlantic off south-west Ireland at a depth of 900 fathoms on *Nuculana pustulosa*.

Bonnevie (1899), in her report on the Hydroida of the Norwegian North Atlantic Expedition, states that the gonophores "probably develop into free medusae", but in her table of species she states that the gonosome is a free-swimming medusa with four radial canals and four tentacles. I can find no reference to this in literature previous to 1899, but all later authors have apparently quoted Bonnevie with respect to the medusa (Broch, 1916; Kramp, 1935).

Sars (1873) and Jäderholm (1909)* are the only authors who have figured this species with medusa buds, but their figures and descriptions are from preserved material. There is no published figure of the liberated medusa. I have therefore thought it desirable to redescribe the species in detail from living material.

Colonies of this hydroid were obtained from two localities at Herdla. Three colonies on *Nucula timidula* were obtained from a depth of 100–200 m. in the Herdlafjord on July 31 1937 by Dr Hult in his "sledge dredge". Dr Hult kindly gave me these colonies for examination, of which two had each a single gonophore. On August 6 1937, about a hundred *Nucula timidula* were obtained by the same apparatus in the Hjeltefjord, south of Toska at a depth of 300–400 m. Twelve of these molluscs had colonies growing on them, but only three colonies carried gonophores.

---

* The hydroid figured by Jäderholm may be a different species.

The stolons form an open network on the surface of the valves of the shell (Fig. 6 *a*). They are of a light brown colour and 0·05–0·07 mm. in diameter. The stems are unbranched rising to a maximum height (to top of hypostome) of 1·1 mm. and are covered by a dark brown or horn-coloured perisarc with adhering mud particles. The perisarc of both hydranth and hydrocaulus is often irregularly wrinkled throughout, but never ringed at the base. It becomes dilated around the base of the hydranth to form a pseudohydrotheca, reaching almost to the base of the tentacles where it thins out and disappears. Too much stress has been laid by some authors on the wrinkling of the perisarc, distinguishing the species by this means from the hydroid of *Leuckartiara octona* (Fleming).

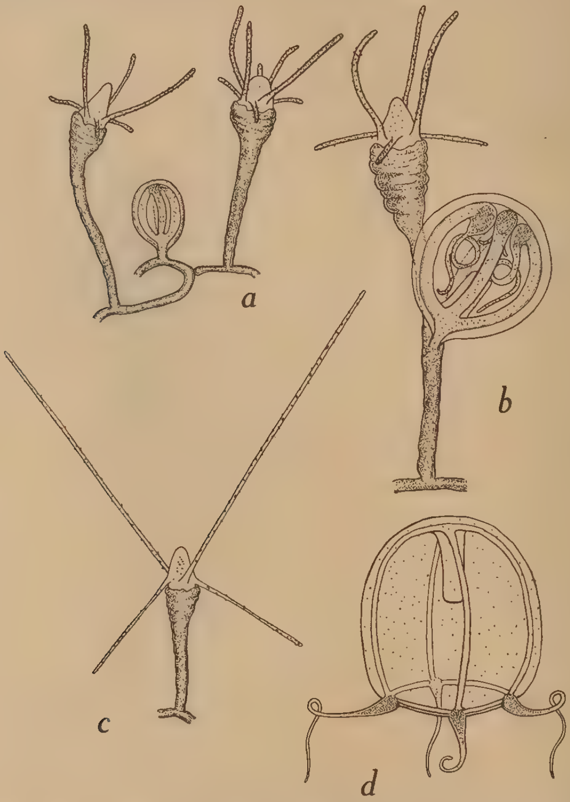


Fig. 6 *a–d*. *Leuckartiara abyssi* (G. O. Sars): *a*, portion of colony with a gonophore developing from the stolon, Herdla, 6. viii. 37; *b*, polyp with a fully developed gonophore on the hydrocaulus, Herdla, 9. viii. 37; *c*, young polyp with its tentacles fully expanded, Herdla, 6. ix. 37; *d*, newly liberated medusa.

Either the very pronounced wrinkling shown in Jäderholm's figure is due to bad fixation or the species figured is distinct from Sars' species. A comparison of Fig. 6 *a–c* with those of the hydroid *Leuckartiara octona* (Figs. 3–5) reveals that the wrinkling of the perisarc cannot be used as a specific character to distinguish the two species.

The hydranth is fusiform or flask-shaped, with a well-developed conical hypostome and a whorl of six to eight filiform tentacles held fairly stiffly, alternately elevated and depressed, the longer tentacles held almost vertical and the shorter ones almost at right angles to the hydrocaulus. Frequently the whole hydranth is so covered with mud particles that only the white tip of the hypostome and the ends of the tentacles can be seen.

The limits of hydranth and hydrocaulus are not clearly marked, the transition being gradual. When extended the tentacles are very thin and the nematocysts appear to be scattered irregularly on them. The fully extended tentacles may reach a length of 1·2 mm. (Fig. 6 *c*).

Only three living colonies with gonophores were found, and in each there was only one developing gonophore.* Sars (1873) also noted that few colonies had gonophores and that in these the gonophores were particularly few.

In two of the colonies the bud was developing from the stolon (Fig. 6 *a*) and in the third from the hydrocaulus. The gonophore developing from the hydrocaulus was in an advanced stage of development (Fig. 6 *b*) when found on August 6 1937. The young medusa bud was covered by a thin hyaline perisarc and was 0·45 mm. long by 0·45 mm. in diameter. It had a very short stalk 0·05 mm. in length. Three days later it had grown to 0·5 mm. long by 0·45 mm. in diameter. The bud was liberated as a free medusa on the same day by rupture of the perisarc.

The newly liberated medusa (Fig. 6 *d*) was of a deep bell shape, 1·15 mm. in height and 1·05 mm. in diameter. It had a fairly thin jelly of uniform thickness with no apical projection. Numerous nematocysts were scattered in the surface of the exumbrella. The velum was present. The stomach was short, quadrangular in section, reaching to about one-third the height of the umbrella cavity. The mouth was simple without distinct lips. The four radial canals and ring canal were fairly broad. There were four perradial tentacles with elongated hollow conical bulbs; of these, two opposite tentacles were better developed than the other two. There were no ocelli, and the colour of the tentacle bulbs and manubrium was a pale yellowish green.

The structure of the newly liberated medusa clearly shows that it belongs to the family Pandeidae. The hydroid appears to be very closely related to the hydroid of *Leuckartiara octona* (Fleming) (=*Perigonimus repens* (Wright, 1857)). The structure of the newly liberated medusa, however, shows it to be quite distinct from this species. The medusa differs from that of *Leuckartiara octona* in having partly developed tentacles on the two smaller perradial bulbs; it is much larger and more globular, there is no apical projection, and the colour is distinct. The species may be the hydroid generation of another species of *Leuckartiara* or possibly *Neoturris pileata* (Forskål). Provisionally at least it appears best to place this species in the medusa genus *Leuckartiara*, as the generic name *Perigonimus* can no longer be used for the hydroids of pandeid medusae. The name of this species therefore becomes provisionally *Leuckartiara abyssi* (G. O. Sars, 1873).

---

* Dr Hult's specimens were already fixed when handed over to me.

Thamnostoma russelli n.sp.

A small hydroid closely resembling *Thamnitis cidaritis** (Weismann 1883) was caught in the Mielck net in the Herdlafjord at a depth of 270 m. on August 31 1937. The species carried medusa buds and in nearly all respects appeared to be almost identical with Weismann's species from the Mediterranean. The structure of the newly liberated medusa, which differed in several respects from that of *T. cidaritis*, indicated that the species can probably be regarded as distinct.

The species described below is a form of some importance in that the structure of its medusa indicates that two medusa genera, at present kept separate, should be united under one genus.

THE HYDROID. The species was a mud-living form anchored in the mud by a twisted network of branching stolons (Fig. 7 *a*). When found the colony was covered with mud with only the tips of the tentacles and the hypostomes of the hydranths visible. The stolons were thin, being 0·05 mm. in diameter. The perisarc of the stolons, the hydrocauli and the hydranths, was of a brownish colour and non-annulated. The polyp stems were unbranched and 2–5 mm. in length with a diameter of 0·10–0·12 mm. They were usually irregularly bent and only occasionally straight.

The hydranths (Fig. 7 *b*) were fusiform, 0·3–0·5 mm. in length and 0·25–0·4 mm. in diameter. They had a single whorl of ten to fifteen filiform tentacles around a conical hypostome. The hydranths were covered by a loose irregularly wrinkled perisarc, which was continued over the body of the hydranth to within a short distance of the mouth and formed a sheath on the proximal portion of each tentacle. This tubular sheath was 0·03 mm. in diameter. The distal end of the tentacle was club-shaped with numerous nematocysts at the tip forming a battery. Each tentacle had an endodermal core consisting of a single row of cells.

The stems carried one, two or three medusa buds on very thin stalks 0·3–0·35 mm. long. Fully grown medusa buds were 0·5–0·55 mm. in length with a diameter of 0·5 mm. The gonophore was covered by a very thin perisarc which was ruptured when the young medusa was liberated.

THE MEDUSA. The newly liberated medusa had a height of 1·2–1·6 mm.

---

* This species was described by Weismann as *Perigonimus cidaritis*. Brückner (1914) redescribed both hydroid and medusa and gave the medusa the name *Thamnitis dichotoma*. Stechow (1919) referred the hydroid to *Thamnitis cidaritis* as the species is clearly not a *Perigonimus*.

and a diameter of 1·2–1·35 mm. (Fig. 7 *c*). The umbrella was deep bell-shaped, a little higher than wide, with a thin jelly of fairly uniform thickness. There was a slight apical projection, and here the jelly was a little thicker than elsewhere. There were a large number of nematocysts scattered over the surface of the exumbrella. The stomach was short, cylindrical and reached to almost one-third of the height of the subumbrella. The mouth was simple with four

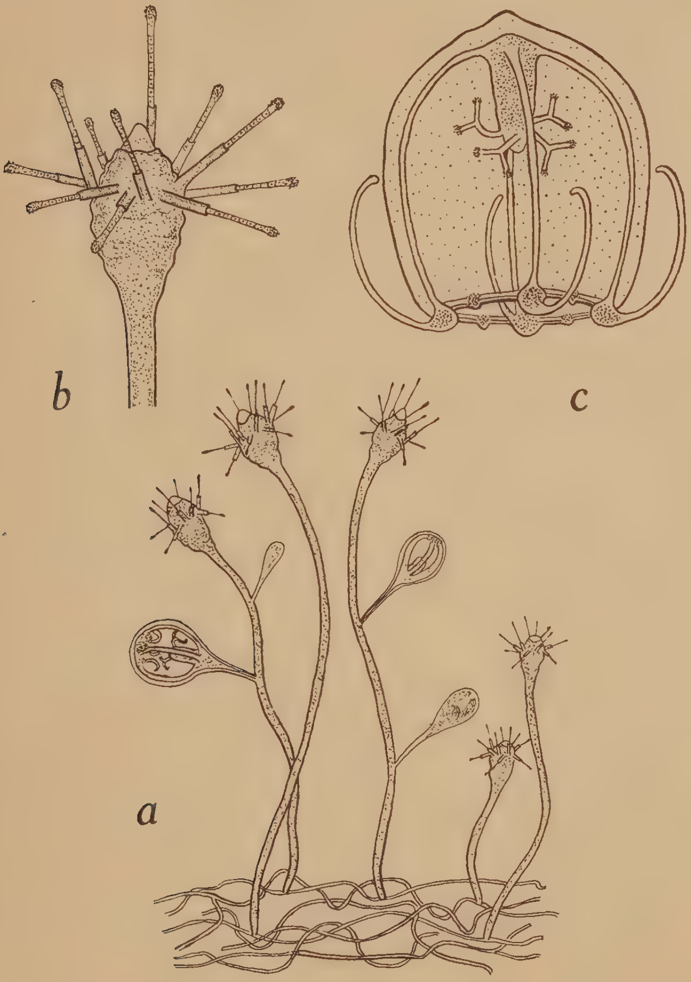


Fig. 7 *a–c*. *Thamnostoma russelli* n.sp.: *a*, colony with medusa buds, Herdla, 6. ix. 37; *b*, single hydranth, Herdla, 1. ix. 37; *c*, newly liberated medusa, Herdla, 2. ix. 37.

branched oral tentacles arising from the manubrium a little above the mouth. Each oral tentacle divided once, each arm having a small battery of nematocysts at its distal end. The radial canals and the ring canal were narrow. There were four well-developed perradial bulbs each with a tentacle and four interradial smaller bulbs without tentacles. There were no ocelli. The tentacle bulbs were yellowish brown in colour, and the base of the stomach was green and its tip reddish brown.

After three days' growth in the laboratory a medusa developed four short interradial tentacles, and the oral tentacles on the manubrium were beginning to branch a second time. The development was not studied further.

This species from Norway is evidently closely related to the Mediterranean species *Thamnitis cidaritis*. The hydroids appear to be almost indistinguishable, but the medusae differ in several respects. Brückner (1914) referred the medusa of the Mediterranean species to the genus *Thamnitis* as *T. dichotoma* on account of the presence of the branched oral tentacles and the four single perradial tentacles. His species differs from my species principally in the absence of interradial bulbs, in its smaller size, and also in the better development of the capitate knobs on the oral tentacles.

Browne (1905) found two small medusae in the Firth of Clyde, Scotland, which he referred to *Thamnitis* as *Thamnitis* sp. Except for the absence of interradial bulbs they appear to be almost identical with my species. The medusa of my hydroid is also related to the medusa *Thamnostoma dibolia* (Busch 1851) from the Gulf of Trieste. This species is only known in the adult stage and nothing is known of its hydroid. It possesses a peculiar spur on the tentacles, and the tentacles also possess ocelli.

It is possible that *Thamnostoma dibolia* and *Thamnitis cidaritis* are stages in the life history of the same species. If this proves to be so then the question whether my species is distinct from *T. cidaritis* will have to be considered. It appears possible that in warm waters the medusae are liberated at an earlier stage of development at which the interradial bulbs have not been developed. For the present it is necessary to keep my species distinct. The close similarity between the hydroid of my species and that of *T. cidaritis*, and the fact that the medusa has more than four tentacles, indicate that the retention of both the generic names *Thamnitis* and *Thamnostoma* is no longer justified. Mayer (1910) placed all the species previously assigned to *Thamnostoma* in the genus *Lymnorea* Péron & Lesueur 1809. Hartlaub (1911) has shown that Mayer draws no distinction between branched oral *lips* and branched oral *tentacles*, and he therefore restricts *Lymnorea* to medusae of the *Podocoryne* type with branched oral lips and numerous marginal tentacles.

Haeckel (1879) placed his genera *Thamnitis* and *Thamnostoma* in his family Thamnostomidae with *T. dibolia* as the genotype of his genus *Thamnostoma*.

Thamnostoma is redefined as follows to include *Thamnitis*:

MEDUSA. Thamnostomid medusae with four or more marginal tentacles and four branched oral tentacles above the mouth.

HYDROID (where known). Stems rarely branched arising from a creeping stolon both covered by a brownish perisarc. Hydranths fusiform, with a single whorl of filiform tentacles around a conical hypostome, covered almost as far as the mouth by an investing perisarc which also forms a sheath around the base of each tentacle. Medusa buds, stalked, borne on the hydrocauli.*

The following species, *Thamnostoma dibolia* (Busch 1851), *T. macrostoma* Haeckel 1879, *Thamnitis tetrella* Haeckel 1879, *T. cidaritis* (Weismann 1883) and *Thamnitis* sp. Browne 1905 can be referred to this genus. To these we must add the new species described above, which I propose to call *Thamnostoma russelli* after Mr F. S. Russell.

The following is a concise definition of this new species:

Thamnostoma russelli n.sp. (Fig. 7)

Stem slender, unbranched, rooted by a tufted mass of thread-like stolons, the whole of the coenosarc enclosed in a brownish non-annulated perisarc; hydranths fusiform, with a single whorl of ten to fifteen filiform tentacles around a conical hypostome, the body and the lower half of each tentacle clothed in a thin perisarc which is irregularly wrinkled on the body of the hydranth. Gonophores medusoid, borne on very slender pedicels on the hydrocauli. Medusa (at liberation) bell shaped, jelly thin, with numerous scattered exumbrellar nematocysts. Umbrella with a slight apical projection. Velum present. Stomach short, cylindrical, with a simple mouth with four dichotomously branched oral tentacles arising above mouth margin. Four radial canals and ring canal narrow. Four perradial marginal tentacles with enlarged basal bulbs and four interradial bulbs with developing tentacles. Tentacular bulbs brownish, stomach green at base, reddish brown distally.

Distribution: Bergen coast (Herdlafjord).

THE HYDROID OF *EUPHYSA AURATA* FORBES 1848

Many specimens of the mud-living hydroid *Corymorpha annulicornis* M. Sars 1859 were obtained at Herdla, and from them young specimens of the medusa *Euphysa aurata* Forbes were liberated. Until recently the hydroid *Corymorpha nana* Alder 1859 has been almost universally accepted as the hydroid of this medusa (e.g. Kramp, 1927; Mayer, 1910). Browne (1896), alone of modern authors, was convinced that it was not the right hydroid of this medusa. The description given by Alder for *C. nana* differs in so many respects from that of *C. annulicornis* that they cannot possibly be the same species. The newly liberated medusae, however, are rather similar, and the medusa of *C. nana* may prove to be another species of *Euphysa*.

---

* There is a close similarity between these two hydroids and *Bimeria vestita* Wright 1859 which has fixed gonophores. It is premature at present to place these species in *Bimeria*. This genus has been united with *Garveia* Wright, which has no tubular perisarc sheaths covering the tentacles of the hydranth, by some authors, e.g. Torrey (1902), Browne (1907), and Stechow (1919), while others, e.g. Fraser (1937), have kept them separate. A revision of the *Bimeria-Garveia* hydroids is greatly to be desired.

Although the figures of both hydroid and medusa are by no means typical, the hydroid, described by E. S. Russell (1906) as *Trichoriza brunnea* (*Rhizotrichia* of Stechow, 1919), is undoubtedly identical with *Corymorpha annulicornis*.

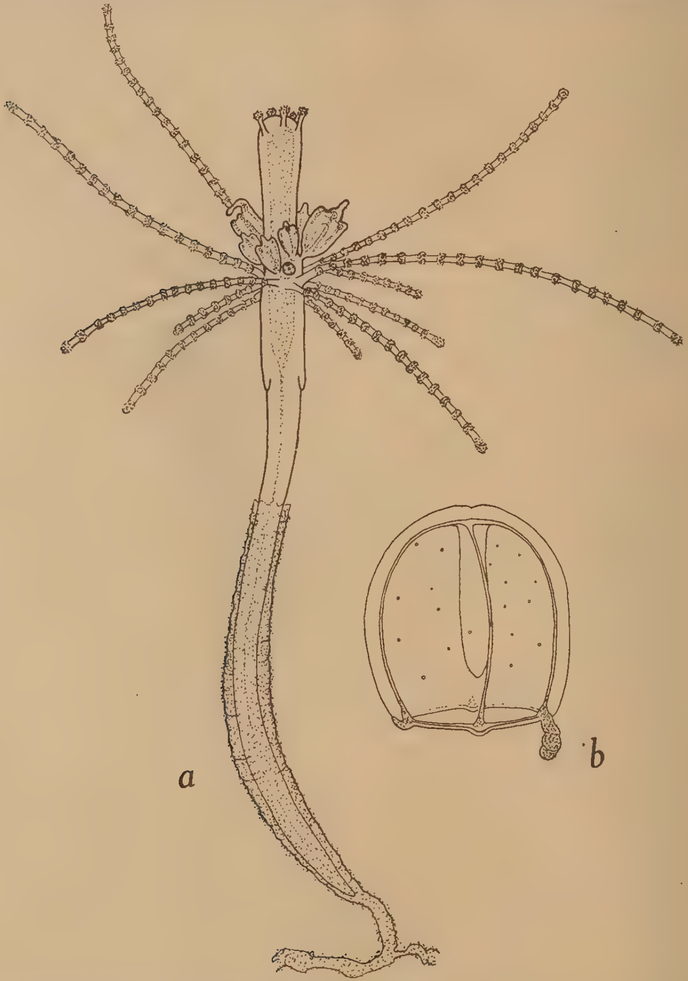


Fig. 8 *a*, *b*. *Corymorpha annulicornis* M. Sars: *a*, expanded polyp with medusa buds, Herdla, 12. viii. 37; *b*, young medusa newly liberated from the hydroid, Herdla, 11. viii. 37.

Having seen young specimens of *C. annulicornis* alive at Herdla I have now no hesitation in referring the specimens I described from Plymouth (Rees, 1937) as *Heterostephanus* sp. to this species.

Dahlgrenella farcta Miles 1937 is very closely related if not identical with *Corymorpha annulicornis*. The validity of the genus *Dahlgrenella* will be discussed later in this paper.

The hydroids were obtained at Herdla with a similar "mud-tangle" apparatus to that described by Miles (1937). The list of localities where the hydroid was found is given below:

9. viii. 37. Ypsøsund, 70 m., 11 specimens.
9. viii. 37. Iø, 20 m., 3 specimens.
9. viii. 37. Rosslandspollen, 30–40 m., 4 specimens.
9. viii. 37. Herdlafjord, 100 m., 2 specimens.
14. viii. 37. Mangerfjord, 200–300 m., 1 specimen.
18. viii. 37. Ypsøsund, 70 m., 33 specimens.
4. ix. 37. Ypsøsund, 70 m., 12 specimens.

The two specimens from the Herdlafjord were obtained by Dr Hult in his "sledge dredge", and the single specimen from the Mangerfjord by washing and sieving the mud from the upper part of the trawl netting. All the other specimens were obtained by dragging the "mud-tangle" along the bottom for 20 min. Each record represents a single haul.

Of all the specimens obtained about 50 per cent carried medusa buds, about 10 per cent were fully grown without buds, and the remainder were young polyps.

Five young hydroids of this species were obtained from Jennycliff Bay, Plymouth Sound, on September 27 1937.

THE HYDROID. The stems are unbranched consisting of a claviform or club-shaped head and a tubular hydrocaulus (Figs. 8, 9). The limits of the hydranth and the stalk are not always clearly marked; in some specimens the head merges imperceptibly into the stalk. The head varies greatly in shape and carries two whorls of tentacles. Some idea of the variation in number of the tentacles and in the size of the medusa-bearing polyps can be obtained from the following table. The measurements are from specimens fixed in Bouin's fluid. When alive the polyps can expand to four or five times the length of the contracted state:

Measurements in mm.

Total length	1·15–4·55
Length of head...	0·6 –1·8
Diameter of head	0·35–0·9
Length of hydrocaulus	0·15–1·8
Diameter of hydrocaulus	0·2 –0·5
Number of oral tentacles	3–8
Number of aboral tentacles	6–14
Number of medusa buds	1–27

The oral tentacles are capitate and generally four in number. The aboral tentacles are moniliform, situated near the posterior end of the hydranth; their usual number is eight to ten.

The aboral tentacles consist of longer and shorter tentacles which alternate and appear to be in two closely approximated whorls, the longer tentacles always arising a little in front of the shorter tentacles. This can only be seen in fully developed individuals. In full-grown polyps bearing medusa buds the number of annulations on each aboral tentacle varies from six to twenty-five. At the posterior end of the hydranth there is a whorl of three to six backwardly directed papillae, and there are also occasionally some on the upper part of the hydrocaulus. One individual had three of these processes, and three other polyps had one each. Similar processes are found scattered on the upper part of the

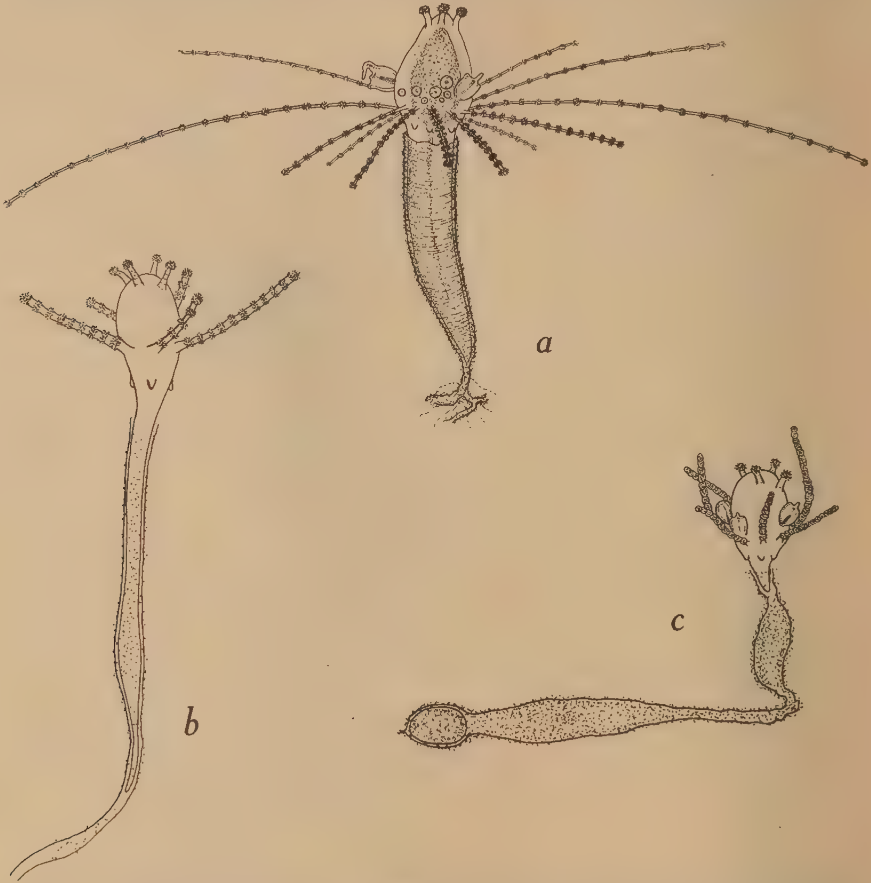


Fig. 9 *a–c*. *Corymorpha annulicornis* M. Sars: *a*, polyp with medusa buds, body contracted, tentacles expanded, Herdla, 10. viii. 37; *b*, young polyp developed by asexual budding from the stolon, Herdla, 9. viii. 37; *c*, polyp with an asexual body in the stolon, Herdla, 4. ix. 37.

hydrocaulus of *Dahlgrenella farcta*; according to Miles (1937) they develop into anchoring filaments, but I saw no indication of this in my specimens. The original specimens taken by Sars near Bergen seem to have been much larger than mine from the same district. His polyps possessed eight to ten oral tentacles, about twenty aboral tentacles and six to eight backwardly directed papillae.

The simple hydrocaulus is covered by a distinct slightly gelatinous membrane which covers the greater part of the hydrocaulus. When the hydrocaulus is expanded the membrane forms a smooth loose-fitting sheath reaching two-thirds of the way up the hydrocaulus; when the hydrocaulus is contracted the membrane contracts with it and appears to be transversely wrinkled. It is almost always covered with fine particles of mud which adhere to it. Below the base of the hydrocaulus the tube may narrow abruptly to form an irregularly branched or unbranched stolon which serves as an anchoring filament. In specimens which have been kept alive in small glass dishes, very thin hair-like anchoring filaments or frustules frequently appear from the posterior fourth of the hydrocaulus and fix the animal securely to the substratum. In the specimens I kept there were never more than ten of these filaments.

Among the eleven specimens obtained from Ypsøsund on August 9 1937 there was one polyp with an asexual bud developing from the body of the hydranth. It was a reversed bud similar to the one described (Rees, 1937) for this species from Plymouth. In this instance no tentacle of the parent polyp was carried away by the bud, which had four oral and four aboral rudiments of tentacles. As in the Plymouth specimen the parent polyp was immature and without gonophores.

The development of young polyps from the stolon is common in this hydroid, and for this Ypsøsund proved to be the most interesting station. Such buds have been described by Broch (1937) for *Corymorpha annulicornis* and by Miles (1937) for *Dahlgrenella farcta*.* Broch notes the presence of a rounded body in the stolon below the hydrocaulus and suggests that it may be a schizospore. In the material from Ypsøsund (September 4 1937) there are several such bodies in the periderm of different polyps. In one the lower part of the hydrocaulus was becoming constricted off (cf. *D. farcta*); in another the proximal end of the periderm contained a rounded body (Fig. 9 *c*). It has already been mentioned that a large percentage of the polyps found were very young ones.

Few, however, of these young polyps were attached by their stolons to the parent polyps, and it is very probable that, in the process of washing and straining the mud, the thin periderm, connecting most of them to their parent polyps, becomes severed.

The youngest polyp still attached to its parent polyp by the periderm possessed four oral tentacles, four aboral tentacles and four backwardly directed processes (Fig. 9 *b*).

* Murbach (1899) has also described such buds in *Hipolytus peregrinus*, a form which approaches nearest to *Corymorpha obvoluta* Kramp and with which it is almost certainly cogeneric.

Measurements of this bud (when alive) are given below:

Measurements in mm.	
Total length	1·75
Length of head	0·65
Diameter of head	0·32
Length of hydrocaulus	1·1
Diameter of hydrocaulus	0·12–0·2

The oldest bud still attached to its parent by the periderm had seven medusa buds and a proximal whorl of ten tentacles.*

Broch (1937) suggests that the British species of *Vorticlava*, *V. humilis* Alder 1856 and *V. proteus* Wright (1863), may possibly be young *Corymorpha annulicornis*, but I cannot agree with this suggestion. Alder and Wright examined their specimens alive, and it is hardly likely that such careful workers would have missed such a striking feature as the annulation of the tentacles had the tentacles been annulated. It appears more likely that these young forms are larval tubularians as suggested by Brink (1925).

SEXUAL REPRODUCTION. The medusa buds are borne singly or in groups of two to six just above the aboral whorl of tentacles. It is questionable whether the small protuberances on which these buds are borne can be called blastostyles. Each bud is naked. It arises as a globular swelling which gradually enlarges, becoming bell-shaped. The manubrium and the four radial canals develop, and at the margin of the bell opposite one of these radial canals a small finger-like tentacle is formed (Fig. 8 *a*). The tentacle as it grows bends inwards like a hook and develops two or three nematocyst batteries. At first its colour is green, but when the medusa is about to be liberated it becomes golden yellow.

When liberated the medusa (Fig. 8 *b*) is of a deep bell shape; the jelly is uniformly thin and there are a few large scattered nematocysts on the exumbrella. The velum is well developed. The stomach is tubular and well developed; the mouth is simple. The stomach is about two-thirds of the length of the subumbrellar cavity. The four radial canals and the ring canal are narrow. There is only one tentacle; this is short and club-shaped when contracted, when expanded it is moniliform, having two or three nematocyst batteries. The tentacle bulbs on the other perradii are small and rudimentary. Each bulb clasps the margin of the bell.

Newly liberated medusae are when alive 0·55–1·0 mm. in height by 0·55–1·0 mm. in diameter. Individual medusae range from brightly coloured specimens to almost colourless ones. The subumbrella and radial canals are faintly pink in some, in others colourless. In brightly coloured medusae the ring canal appears as a crimson circle. There is always a crimson pigment spot at the tip of the manubrium, the remainder is yellow, sometimes with brownish pigment at the base. The upper part of the tentacle bulbs including the junction of the radial and ring canals is vivid scarlet or crimson with a few black pigment granules at the ends of the radial canals. The single tentacle is golden yellow in colour and the lower part of the tentacle bulbs which clasp the margin are also yellow.

---

* Since this paper was written I have received from Dr Hult a species of *Corymorpha* obtained in the Trondheimsfjord from a depth of about 480 m. It approaches very near to and may be identical with *C. annulicornis*. It is much larger than my Herdla specimens, having a total length of 9·5 mm. There are well-developed *branched* blastostyles bearing gonophores which are distinctly medusoid in form. Without more knowledge of the gonophore, however, I prefer not to refer this specimen to *C. annulicornis*.

The newly liberated medusae and the various stages seen in the townets at Herdla confirm Broch's opinion that this species is identical with *Euphysa aurata* Forbes. The newly liberated medusae (of which one was captured in the townets) correspond to those described by Browne (1896). Browne states that: "The shape of the umbrella, of the tentacle bulbs, and of the large tentacle is similar in all stages: thus there is no difficulty in identifying the earliest forms."

The youngest stage captured in the Herdlafjord on September 2 1937 was obviously a newly liberated specimen and differed in no way from those already described. It was 0·75 mm. in height by 0·7 mm. in diameter.

A slightly older specimen caught in the Hjeltefjord on September 23 1937 possessed a slightly thicker jelly and a slightly longer tentacle. It was immature and was 1·1 mm. high and 1·05 mm. in diameter.

A ripe male medusa was obtained in a haul in the Hjeltefjord south of Toska on September 21 1937. It only differed from specimens previously described here in its greater size, greater thickness of jelly, length of tentacle and the presence of the gonad on the manubrium. It was 2·5 mm. high by 2·0 mm. in diameter.

Euphysa aurata is the only species of its genus with the same distribution as the hydroid *Corymorpha annulicornis*. According to Kramp (1927) the medusa occurs from the English Channel to the Murman coast. It has also been reported from Greenland (Kramp, 1926) and from the Mediterranean. It is very common along the Scottish coasts and along the Norwegian coast.

The records of the hydroid are few, probably because the species is a mud-living form and necessitates a special apparatus to catch it. Sars (1859) found two species at Flören (Sondfjord) in the Bergen district. Russell (1906) has recorded it from the Firth of Clyde as *Trichorhiza brunnea*, and the present writer has found it abundant at Herdla (Bergen), and also less commonly at Plymouth.

The only other north European species of *Euphysa* is *E. tentaculata* (Linko 1904) which is only known from the Barents Sea and a few localities in the southern Kattegat and the Belt Sea (Kramp, 1927).

It is therefore almost certain that the medusa *E. aurata* can be linked with the hydroid *Corymorpha annulicornis*.

The species was originally described by Michael Sars (1859) as *C.* ? *annulicornis*: Sars himself was doubtful which generic name this species should bear. Allman (1864 *a*) erected the genus *Heteractis* (later he changed it to *Heterostephanus*) for this species because of the peculiar ringed nature of the proximal tentacles. Recently the species has been redescribed by Broch as *Corymorpha* (*Euphysa*) *annulicornis*. This raises the question of what name the species should bear.

The capitate oral tentacles, the moniliform aboral tentacles, the backwardly directed papillae, the few frustules, the almost sessile gonophores and the characters of the medusa all apparently justify the separation of this species from *Corymorpha*. Indeed, the medusae have been kept under different genera, viz. *Corymorpha* (*Steenstrupia*) and *Euphysa*.

The separation seems justified when we compare the hydroid of *C. nutans* with the hydroid of the present species, but if all other species of *Corymorpha* are taken into consideration it appears evident that the so-called generic characters of *Heterostephanus* are possessed by other species of *Corymorpha*.

C. obvoluta Kramp 1933 possesses, like *C. annulicornis*, moniliform proximal tentacles, sessile gonophores and backwardly directed papillae. It differs in having (among other characters) fixed gonophores, a well-developed periderm and moniliform oral tentacles. The relations of *C. obvoluta* to other Corymorphinae has been fully discussed by Kramp (1933), and so they need not be discussed here.

The chief difference distinguishing medusae of the genus *Steenstrupia* from *Euphysa* is the presence of an apical projection to the umbrella which is perhaps more suitable as a specific character than as a generic one.

It may be that all species of *Euphysa* are liberated from *Corymorpha* hydroids with moniliform aboral tentacles, but at present it is premature to lay too much stress on the significance of these annulations because the hydroids of all *Euphysa* medusae (except *Corymorpha annulicornis* and *Dahlgrenella farcta*) are unknown. For the present there is no justification for separating *Euphysa* from *Corymorpha*, and the species described here has been referred to as *C. annulicornis*. Now that the hydroid has been linked with the medusa *Euphysa aurata* Forbes the name of both hydroid and medusa must become *Corymorpha aurata* (Forbes 1848)* if the dual classification is eventually superseded.

Miles (1937) founded his genus *Dahlgrenella* chiefly on the peculiar asexual reproduction of his hydroid. It has been shown by Broch (1937) and in the present paper that budding from the stolon takes place normally in *Corymorpha annulicornis*, and there is now no reason why the species should not be included in the genus *Corymorpha* as *C. farcta*. Even if it should become necessary to remove these species from *Corymorpha*, then the claims of *Euphysa* Forbes 1848 and *Heterostephanus* Allman 1864 would have priority over *Dahlgrenella* Miles 1937, and also over *Hipolytus* Murbach 1899. The medusa liberated from *Corymorpha farcta* is a typical *Euphysa* and may possibly be the immature stage of *E. virgulata* A. Agassiz 1865 which is common along the American North Atlantic coast. Opinion is divided as to whether this species is distinct from *E. aurata* (see Mayer, 1910, p. 35). The hydroids *Corymorpha annulicornis* and *C. farcta* are very closely related and may prove to be identical.

---

* *Corymorpha* Sars 1835 has priority over *Euphysa* Forbes 1848, and the species name "*aurata*" Forbes 1848 has priority over "*annulicornis*" Sars 1859.

Campanulina paracuminata n.sp.

A small colony of a *Campanulina* was found on a clinker trawled in the Cattewater, Plymouth, on February 4 1936. As the colony was not reproducing it was kept in a finger bowl and fed at intervals. On October 3 the colony was transferred to the apparatus described by Rees & Russell (1937). Here the polyps were able to feed more satisfactorily and more rapidly, and by March 7 1937, more than a year after its capture, the colony was in a thriving condition with about fifty hydranths. Gonophores were observed for the first time on April 15 1937, and two days later medusae were liberated.

The trophosome of the hydroid appeared to be almost identical with *Campanulina acuminata* (Alder), but my colony was less branched than the latter and very rarely possessed more than two polyps on the same hydrocaulus. The structure of the newly liberated medusa showed that the hydroid was distinct from *C. acuminata*.

The Hydroid. The stems were slender rising to a height of 1·5–2·5 mm. from a branched creeping stolon. The stems were imperfectly annulated throughout their length, being 0·05 mm. in diameter. The hydrocaulus carried one or two hydranths, the second hydranth usually arising just below the hydrotheca of the terminal hydranth. The hydrothecae were cylindrical, square below and tapering to a fine point above (Fig. 10 *a*). Their perisarc was thin and finely striated along their length; they were 0·38–0·42 mm. long by 0·09–0·1 mm. wide. The hydranth was very extensile and might extend to a height of 1·1 mm. from the base of the hydrotheca. There were about twenty tentacles around the base of a bluntly conical hypostome. These were united at the base by a well-developed membranous web. This web usually contained a number of large bean-shaped nematocysts approximately 0·015 mm. in length (Fig. 10 *b*). With chlorazol black E these bodies stain a dense blue-black and can then be seen in numbers scattered in the coenosarc of the stolon and hydrocaulus and also in the body. Their number and arrangement was never constant; very few were present in the earliest polyps seen. The tentacles extended to a maximum length of 0·6 mm. They had an endodermal core of a single row of cells, and the nematocysts were irregularly distributed. The hydranths could not be distinguished from those of *Campanulina acuminata* with which they were compared in the living condition. Both colonies were grown in the laboratory, and their mode of branching may not be typical of colonies obtained from nature.

Gonophores were observed on April 15. These were borne on the hydrocauli just below the hydranths (Fig. 10 *a*). The fully developed gonophores were large and cylindrical and attached to the hydrocaulus by an imperfectly ringed stalk of varying length (but always shorter in length than the gonotheca itself).

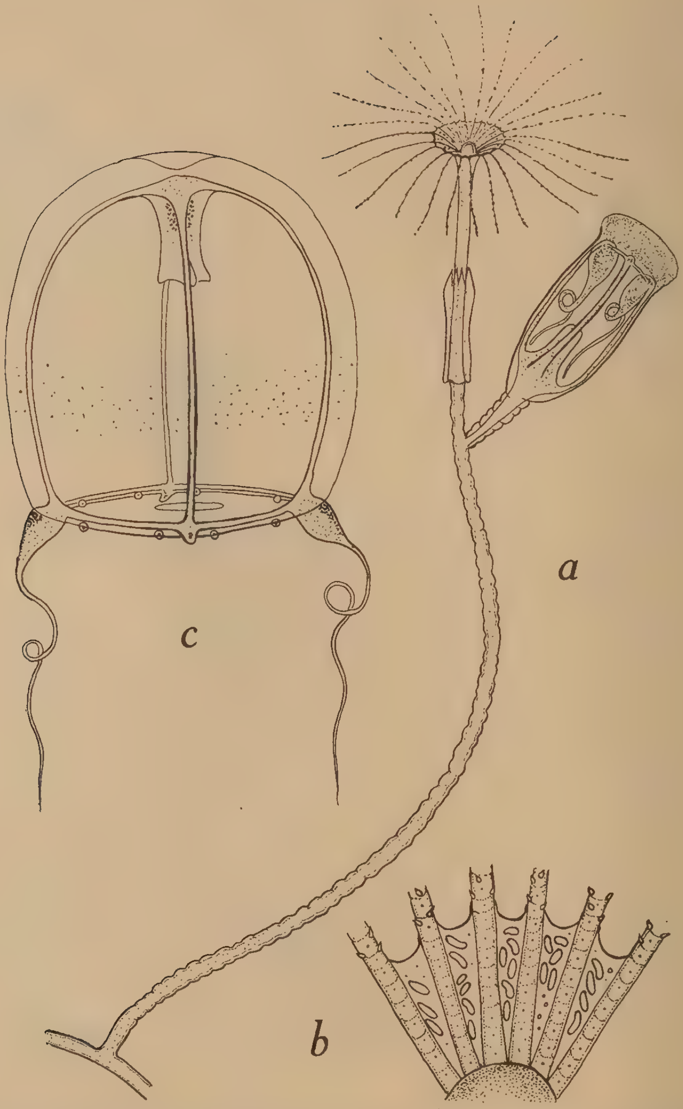


Fig. 10 *a–c*. *Campanulina paracuminata* n.sp.: *a*, single polyp with a fully developed gonophore, Plymouth, 4. ii. 37; *b*, a small portion of the web of a hydranth showing the bean-shaped nematocysts, Plymouth, 20. iii. 37: *c*, newly liberated medusa with a diameter of 1·1 mm., Plymouth, 22. ii. 37.

The gonotheca and stalk were 0·75–1·1 mm. in length, while the diameter was 0·3–0·4 mm. The gonophore contained one medusa (rarely two), borne on a thin blastostyle which enlarged distally to form a distinct cap to the gonotheca. When fully developed the medusa escaped from the gonotheca partially by its own efforts and by partial collapse of the thin membranous gonotheca which regained its shape once the medusa came out.

THE MEDUSA. The newly liberated medusa was of a deep bell shape a little higher than wide (Fig. 10 *c*). It was 1·4 mm. high and 1·1 mm. in diameter. The jelly was moderately thick and had a slight depression at the apex. There was a conspicuous band of nematocysts on the exumbrella just below the middle or widest part. The velum was broad. The stomach had a slight apical projection; it was short and quadrangular in section; the mouth had four simple lips. The four radial canals and ring canal were narrow. There were two opposite perradial tentacles with elongated bulbs and two smaller perradial opposite bulbs without tentacles. There were eight closed globular marginal vesicles, adradial in position, each with a single concretion. There were no excretory pores.

This species is more closely related to *Campanulina acuminata* (Alder 1857) than to any other known species of *Campanulina*. *C. tenuis* van Beneden 1847 was regarded by Alder as identical with his *C. acuminata*, but even if (judging from van Beneden's figures) it may possibly prove to be distinct from *C. acuminata*, it is certainly quite distinct from my species. A comparison of the trophosome of my species with that of living *C. acuminata*, kindly sent to Plymouth from Cullercoats by Dr H. O. Bull, revealed no visible difference between the trophosome of the two species. The *C. acuminata* sent by Dr Bull was kept for six months under the same conditions as my species. Both colonies produced gonophores at the same time and so it was possible to compare the newly liberated medusae. The essential differences between the two species are indicated below.

	Campanulina acuminata (Alder) Medusa	*Campanulina paracuminata* n.sp. Medusa
Umbrella.	Deep bell-shaped with a fairly thick jelly. No apical depression.	Deep bell-shaped a little higher than wide; jelly less thick. Apical depression present.
Nematocysts.	Scattered over the whole exumbrella.	Confined to a band around the lower middle part of the exumbrella.
Colour of subumbrella.	Vivid yellowish green.	Vivid bluish green.
Colour of stomach.	Colourless.	Reddish yellow.
Colour of tentacles.	Yellow with two lateral strips of blue-black.	Yellow with a single central strip of blue-black pigment.
Height.	1·6 mm.	1·4 mm.
Diameter.	1·6 mm.	1·1 mm.

Wright (1861) reared the first polyps of a webbed *Campanulina* hydroid from the planulae of *Aequorea vitrina* Gosse. He declared that, as far as he could recall, the young form which he reared from *A. vitrina* was identical with the hydroid of *Campanulina acuminata*. Strong (1925) has reared the first polyps of an *Aequorea*, *A. victoria* (Murbach & Shearer 1903), giving the hydroid the name *Campanulina membranosa*.

I am much indebted to Mr F. S. Russell for permission to make use of his unpublished observations on the life history of *C. acuminata*. Several young medusae found in the plankton at Plymouth, corresponding to the newly liberated medusae of *C. acuminata* but in later stages of development, leave no doubt that the medusa develops into a species of *Aequorea*. One specimen found on May 23 1934 was 1·8 mm. high by 2·5 mm. wide and had a bell-shaped umbrella a little wider than high and a fairly thick jelly of uniform thickness. It possessed four radial canals, four fully developed tentacles, four small interradial tentacles and eight adradial rudiments. The stomach was short, quadrangular in section, with four simple well-developed oral lips. In colour it agreed exactly with the newly liberated medusa of *C. acuminata*.

Another specimen found on November 7 1935 was 4·1 mm. in diameter. It was in a much more advanced stage than the previous specimen. The umbrella was dome-shaped with a thick apical jelly becoming thin towards the margin. The stomach reached to about half the height of the subumbrellar cavity and its oral lips were further developed. It possessed eight complete radial canals and eight developing canals. There were four radial tentacles, four interradial tentacles, eight adradial tentacles and sixteen rudiments of tentacles between every two tentacle bulbs. The marginal vesicles were twenty-six in number with concretions varying from one to four in number. The subumbrella was a bright yellowish green in colour, and the tentacle bulbs were yellow with two lateral strips of blue-black pigment. The specimen had the appearance and characters of young *Aequorea* and was identified as such. *Campanulina acuminata* and the hydroid of *Aequorea vitrina* are sufficiently related to *Campanulina paracuminata* n.sp. to permit the supposition that the medusa liberated from *C. paracuminata* develops into a species of *Aequorea*. Our knowledge of the various species of *Aequorea* is still very unsatisfactory, and I have therefore placed this species provisionally in the genus *Campanulina* van Beneden 1847 as defined by Hincks (1868).*

The species may be defined as follows:

Campanulina paracuminata n.sp.

Stem slender, more or less branched, imperfectly annulated throughout, branches developed on the hydrocaulus a little below the hydranth. Hydrothecae thin, membranous, finely striated longitudinally, elongate pod-shaped, square below and tapering to a fine point above. Polyps extensile with about twenty tentacles, united for about one-fifth of their length by a membranous web with bean-shaped nematocysts embedded in it.

---

* It is not proposed here to discuss the various so-called species of *Campanulina* which have been referred to this genus.

Gonothecae large, cylindrical, with an imperfectly ringed stalk, borne laterally on the primary stems.

Medusa, pale bluish green, umbrella deep bell-shaped, a little higher than wide with a band of nematocysts confined to the lower middle part of the subumbrella and with an apical depression. Stomach short, quadrangular, with four simple lips. Two opposite marginal tentacles and two bulbs without tentacles; bulbs yellow with a single central strip of blue-black pigment. Marginal vesicles adradial, each with one concretion.

Notes on other Hydromedusae

Boreohydra simplex Westblad 1937.

Ten specimens of this interesting hydroid were collected on August 9 1937 at Ypsøsund, Herdla, at a depth of 70 m. The specimens were 1·0–1·75 mm. in length and the oral tentacles were four in number. Except for their slightly greater size, the specimens differed in no respect from the description given by Westblad (1937). He found the species in two localities on the Norwegian coast, in the Ramfjord and at Tromsö. Eleven specimens were found by Dr Jöran Hult in the Balsfjord, Tromsö; they were identical with my species from Herdla.

Stauridium productum Wright 1858.

Synonyms: *Coryne cerberus* Gosse 1853.
Perinema cerberus Stechow 1923.

A colony of this hydroid was grown from a stolon on a stem of *Tubularia indivisa* obtained at Bognøstrømmen on August 14 1937. The stem of the *Tubularia*, which also had other hydroids growing on it, was placed in a similar apparatus to that described by Rees & Russell (1937), which Professor Brinkmann had specially set up for my use. The polyps which I reared from this colony at Herdla and later at Plymouth* were very similar to those figured by Hartlaub (1895). The development of the hydranth is quite distinct from that of *Staurocoryne filiformis* Rees 1936. The developing hydranth first grows three or four capitate oral tentacles, and next the four or five filiform tentacles at the proximal end are developed (Fig. 11 *a*). At this stage the hydranths look exactly like *Coryne cerberus* Gosse, and I agree with Hartlaub that the two species are identical. The young hydranth corresponding to *C. cerberus* had a length of 0·25 mm. and a diameter of 0·11 mm. Additional whorls of tentacles (rarely more than one or two) are developed between the oral whorl and the filiform whorl. In the colony I reared, most hydranths never developed more than two whorls of capitate tentacles (Fig. 11 *b*). The oral whorl developed five or six tentacles in all; this agrees with Hartlaub's observations on this species. No medusa buds have developed to date (28. ii. 38).

---

* Three species of hydroid were brought back to Plymouth from Herdla in a thermos flask. These were *Bougainvillia muscoides*, *Stauridium productum* and a species of *Syncoryne*; they are still alive in my beakers (28. ii. 38).

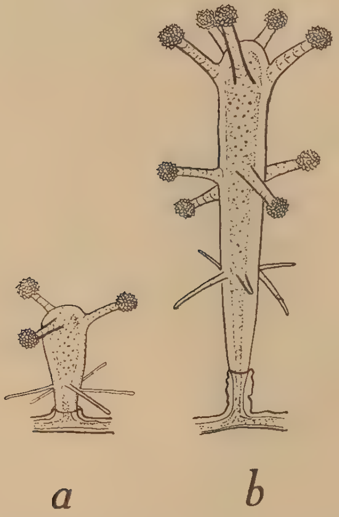


Fig. 11 *a*, *b*. *Stauridium productum*: *a*, young hydranth, Herdla, 20. viii. 37; *b*, fully developed hydranth, Herdla, 20. viii. 37.

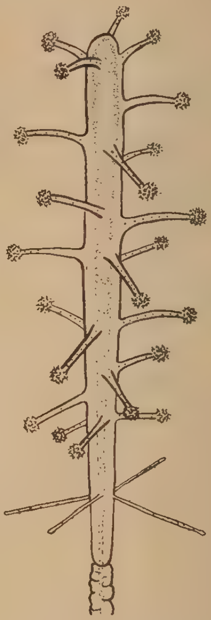


Fig. 12. *Staurocoryne filiformis*; single hydranth, Plymouth, 5. iv. 37.

Measurements of this colony are given below:

Measurements in mm.

Length of hydranth	1·0 –1·8
Diameter of hydranth	0·15–0·23
Diameter of hydrocaulus	0·10
Diameter of stolon	0·15
Total length of oral tentacle	0·20–0·3

The trophosome of the hydroid can easily be distinguished from *Staurocoryne filiformis* by its more delicate growth, the smaller hydranths, the few whorls of tentacles and by the development of the whorl of filiform tentacles immediately after the oral whorl.

Staurocoryne filiformis Rees 1936.

A small colony of this hydroid was found on a *Pecten* shell dredged from New Grounds, Plymouth Sound, on March 16 1937. Previously this hydroid was only known from a colony reared in the Plymouth Laboratory (Rees, 1936). The colony from nature differed from that reared in the laboratory only in the slightly smaller size of the hydranths and in the more irregular distribution of the tentacles (Fig. 12). There were four filiform tentacles which later increased to five in number. They carried a few scattered nematocysts. Identification was verified when the colony developed styloid gonophores two months later.

SUMMARY

The newly liberated medusa of *Perigonimus muscoides* M. Sars has been found to be a *Bougainvillia*. A specimen from the plankton points to the extreme probability that it can be regarded as synonymous with a previously described medusa, *B. nordgaardi* (Browne). The name of both hydroid and medusa now becomes *B. muscoides* (M. Sars 1846).

The systematic importance of the above discovery is discussed, and the genus *Rhizorhagium* M. Sars 1877 is redefined to include all those species of "*Perigonimus*" with fixed gonophores, viz. *Rhizorhagium roseum*, *R. sarsi*, *R. antarcticum*, *R. formosum*, and a new species, *R. album*, from the Cornish coast.

Variations in the form of the hydroid of *Leuckartiara octona* are described. The newly liberated medusa of *Perigonimus abyssi* G. O. Sars is figured for the first time and the species referred to the genus *Leuckartiara*.

A new *Bimeria*-like hydroid, *Thamnostoma russelli*, is described. The characters of the medusa indicate that it belongs to the genus *Thamnostoma* Haeckel, and the characters of the hydroid show that the genera *Thamnitis* and *Thamnostoma* must be united.

Corymorpha annulicornis M. Sars is redescribed from living specimens and the medusa is shown to be *Euphysa aurata* Forbes. It must henceforth be known as *Corymorpha aurata* (Forbes).

A new species of *Campanulina*, *C. paracuminata*, with its young medusa is described from Plymouth.

Notes are included on *Boreohydra simplex*, *Stauridium productum* and *Staurocoryne filiformis*.

Certain points in the synonymy of all these species are discussed.

REFERENCES

AGASSIZ, A., 1865. Illustrated catalogue of the Museum of Comparative Zoology at Harvard College. No. II. *North American Acalephae*, pp. 1–234.

ALDER, JOSHUA, 1857. A catalogue of the zoophytes of Northumberland and Durham. *Trans. Tyneside Nat. Field Club*, Vol. III, pp. 93–162.

— 1862. Supplement to a catalogue of the zoophytes of Northumberland and Durham. *Trans. Tyneside Nat. Field Club*, Vol. v, pp. 225–47.

ALLMAN, G. J., 1863. Notes on the Hydroida. *Ann. Mag. Nat. Hist.*, Ser. 3, Vol. XI, pp. 1–12.

— 1864 *a*. On the construction and limitation of genera among the Hydroida. *Ann. Mag. Nat. Hist.*, Ser. 3, Vol. XIII, pp. 345–80.

— 1864 *b*. Notes on the Hydroida. *Ann. Mag. Nat. Hist.*, Ser. 3, Vol. XIV pp. 57–64.

ALLMAN, G. J. 1871–2. *A Monograph of the Gymnoblastic Hydroids*, pp. 1–450. Ray Society.

BENEDEN, P. J. VAN, 1866. Recherches sur la faune littorale de Belgique. *Mém. Acad. R. Belgique*, Tome XXXVI, pp. 1–207.

BONNEVIE, KRISTINE, 1898. Neue norwegische Hydroiden. *Bergens Mus. Aarb.*, 1898, No. V, pp. 1–15.

— 1899. Hydroida. *Norwegian North-Atlantic Expedition* 1876–1878, pp. 1–103. Christiania.

BRINK, A., 1925. Beiträge zur Herstellung einer rationellen Hydroidensystematik. *Tijdschr. ned. dierk. Ver.*, Ser. 2, Vol. XIX, Pts. 3–4, pp. 126–65.

BROCH, HJALMAR, 1905. Nordsee-Hydroiden. *Bergens Mus. Aarb.*, 1905, No. VI, pp. 1–25.

— 1909. Die Hydroiden der arktischen Meere. *Fauna Arctica*, Bd. V, Jena, pp. 127–248.

— 1911. Fauna droebachensis. 1. Hydroider. *Nyt. Mag. f. Naturvid.*, Bd. 49, Kristiania, pp. 1–46.

— 1916. Hydroida (Part I). *Danish Ingolf-Expedition*, Vol. V, pp. 1–66. Copenhagen.

— 1928. Hydrozoa, I. *Die Tierwelt der Nord- und Ostsee*, Lief. XIII, Teil III *b*, pp. 1–94.

— 1937. Hydroidenuntersuchungen. VII. *Corymorpha (Euphysa) annulicornis* M. Sars 1859. *Norske Videnskaps-Acad. Oslo* I. *Mat.-Naturv. Klasse*, 1937, No. 8, pp. 1–32.

BROWNE, E. T., 1896. On British hydroids and medusae. *Proc. Zool. Soc.* London, pp. 459–500.

— 1903. Report on some medusae from Norway and Spitzbergen. *Bergens Mus. Aarb.* 1903, No. IV, pp. 1–36.

— 1905. A report on the medusae found in the Firth of Clyde (1901–1902). *Proc. Roy. Soc.* Edinburgh, Vol. XXV, pt. IX, pp. 738–78.

— 1907. The hydroids collected by the *Huxley* from the north side of the Bay of Biscay in August 1906. *Journ. Mar. Biol. Assoc.*, Vol. VIII, No. 1, pp. 15–36.

BRÜCKNER, ERICH, 1914. Beitrag zur Kenntnis von *Perigonimus cidaritis* Weisman, und *Gemmaria implexa* var. *neapolitana* Hargitt. *Z. wiss. Zool.* Leipzig, Bd. CXI, pp. 445–505.

BUSCH, WILHELM, 1851. *Beobachtungen über Anatomie und Entwickelung einiger Wirbellosen Seethiere*, pp. 1–143. Berlin.

CALKINS, G. N., 1899. Some hydroids from Puget Sound. *Proc. Boston Nat. Hist. Soc.*, Vol. XXVIII, pp. 333–67.

FEWKES, J. W., 1889. New Invertebrata from the coast of California. *Bull. Essex Inst.*, Vol. XXI, pp. 99–146.

FORBES, EDWARD, 1848. *A Monograph of the British naked-eyed Medusae*, pp. 1–104. Ray Society.

FRASER, C. MCLEAN, 1937. *Hydroids of the Pacific Coast of Canada and the United States.* Univ. Toronto Press.

GOSSE, P. H., 1853. *A Naturalist's Rambles on the Devonshire Coast*, pp. 1–448. London: John van Voorst.

GUDGER, E. W., 1928. Association between Sessile Colonial Hydroids and Fishes. *Ann. Mag. Nat. Hist.*, Ser. 10, Vol. I, pp. 1–48.

HAECKEL, ERNST, 1879. *Das System der Medusen*, pp. 1-672.

HARTLAUB, C., 1895. Polypen und Quallen von *Stauridium productum* Wright und *Perigonimus repens* Wright. *Zeit. f. wiss. Zool.*, Bd. LXI, pp. 142–62.

— 1911. *Nordisches Plankton.* Lief. 6, XII, Craspedote Medusen. Teil 1, Lief. 2, Familie III, Margelidae, pp. 137–235.

— 1914. *Nordisches Plankton.* Lief. 6, XII, Craspedote Medusen. Teil 1, Lief. 3, Familie IV, Tiaridae, pp. 237–363.

HEATH, HAROLD, 1910. The association of a fish with a hydroid. *Biol. Bull.*, Vol. XIX, No. 2, 1910, pp. 73–8.

HICKSON, S. J. & GRAVELY, F. H., 1907. Coelenterata II. Hydroid zoophytes. *Nat. Antarct. Exped.*, 1901–4, *Nat. Hist.* III, London, Brit. Mus., 34 pp. 4 pls.

HINCKS, THOMAS, 1868. *A History of the British Hydroid Zoophytes*, pp. 1–338. London: John van Voorst.

JÄDERHOLM, E., 1909. Northern and Arctic invertebrates in the collection of the Swedish State Museum. IV. Hydroiden. *Kungl. Svenska Vetenskap. Handl.*, Bd. 45, No. 1, pp. 1–124.

KRAMP, P. L., 1911. Reports on the hydroids collected by the Denmark Expedition at north-east Greenland. *Danmark-Eksped. til Grönlands Nordöstkyst* 1906–8, Bd. 5, Köbenhavn.

— 1914. Conspectus Faunae Groenlandica. Hydroider. *Meddel. om Grönland*, XXIII, Köbenhavn.

— 1926. Medusae. Part II. Anthomedusae. *Danish Ingolf-Expedition*, Vol. V, Part 10, pp. 1–102.

— 1927. The Hydromedusae of Danish waters. *Mem. Acad. Sci. Lett. Danemark, Sect. Sci.*, Ser. 8, Tome XII, No. 1, pp. 1–290.

— 1932*a*. The Godthaab Expedition, 1928. Hydroids. *Meddel. om Grønland*, Bd. 79, No. 1, pp. 1–86.

— 1932*b*. Hydroids collected in west Greenland fjords in 1911 and 1912. *Meddel. om Grønland*, Bd. 91, No. 3, pp. 1–34.

— 1933. Coelenterata, Ctenophora and Chaetognatha. *Meddel. om Grønland*, Bd. 104, No. 11, pp. 1–20.

— 1935. Polypdyr (Coelenterata). I. Ferskvandspolypper og Goplepolypper. *Danmarks Fauna*, 41, pp. 1–207, Figs. 1–81.

— 1937. Polypdyr (Coelenterata). II. Golper. *Danmarks Fauna*, 43, pp. 1–223, Figs. 1–90.

— 1938. Marine Hydrozoa. Hydroida. *The Zoology of Iceland*, Vol. II, Pt. 5a. Copenhagen.

KRAMP, P. L. & DAMAS, D., 1925. Les Méduses de la Norvège. *Vidensk. Medd. Dansk naturh. Foren.* Bd. 80, pp. 217–324.

LELOUP, E., 1932. Une collection d'Hydropolypes appartenant á l'Indian Museum de Calcutta. *Rec. Indian Museum*, Vol. XXXIV, Part II, pp. 131–70.

LEVINSEN, G. M. R., 1892. Om Fornyelsen af Ernaeringsindividerne hos Hydroiderne. *Vidensk. Medd. Dansk naturh. Foren.* Kjöbenhavn, pp. 12–31.

— 1893. Meduser, Ctenophorer og Hydroider fra Grönlands Vestkyst. *Vidensk. Medd. Dansk naturh. Foren.* Kjöbenhavn, pp. 1–70.

LINKO, A., 1904. Zoologische Studien im Barents-Meere. *Zool. Anz.*, Bd. XXVIII, pp. 210–20.

MAYER, A. G., 1910. *Medusae of the World.* Vol. I. *Hydromedusae*, pp. 1–230.

MILES, S. S., 1937. A new genus of hydroid and its method of asexual reproduction. *Biol. Bull.*, Vol. LXXII, pt. 3, pp. 327–33.

MURBACH, L., 1899. Hydroids from Wood's Hole, Mass. *Hipolytus peregrinus*, a new unattached Marine Hydroid: *Corynitis Agassizii* and its medusa. *Quart. Journ. Micr. Sci.*, London, Vol. XLII, pt. 3, N.S., pp. 341–60.

NEPPI, VALERIA & STIASNY, GUSTAV, 1913. Die Hydromedusen des Golfes von Trieste. *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Trieste*, Bd. XX, pp. 23–90.

REES, W. J., 1936. On a new species of hydroid *Staurocoryne filiformis*, with a revision of the genus *Staurocoryne* Rotch 1872. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 135–42.

— 1937. On a remarkable process of bud formation in a gymnoblastic hydroid (*Heterostephanus* sp.). *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 747–52.

REES, W. J. & RUSSELL, F. S., 1937. On rearing the hydroids of certain medusae, with an account of the methods used. *Journ. Mar. Biol. Assoc.*, Vol. XXII, No. 1, pp. 61–82.

RITCHIE, JAMES, 1913. A New British commensal hydroid, *Perigonimus abyssi* G. O. Sars. *Fisheries Ireland Sci. Invest.* 1913, I, 1913, pp. 1–3.

RUSSELL, E. S., 1906. On *Trichorhiza*, a new hydroid genus. *Proc. Zool. Soc.*, London, February 1906, pp. 99–101.

— 1907. The *Atractylis coccinea* of T. S. Wright. *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. XX, pp. 52–5.

SARS, MICHAEL, 1835. *Beskrivelser og Iagt*, etc., pp. 1–81. Bergen.

— 1846. *Fauna Littoralis Norvegiae*, I, pp. 1–94. Christiania.

— 1857. Bidrag til kundskaben om Middelhavets Litoral-Fauna. *Nyt. Mag. Naturvid.*, Vol. IX, pp. 110–64.

— 1859. Udtog af en Afhandling, etc. *Forhandl. i Vid. Selsk. i Christiania*, 1859, pp. 96–105.

— 1877. New and little known Coelenterates. *Fauna Littoralis Norvegiae*, III, pp. 1–48, Taf. 1–2.

SARS, G. O., 1873. Bidrag til Kundskaben om Norges Hydroider. *Vidensk.-Selsk. Forhandl.* for 1873, pp. 1–62.

SCHYDLOWSKY, A., 1901. Les Hydraires de la Mer Blanche le long du littoral des Iles Solowetzky. *Trav. Soc. Nat. Univ. Imp. Kharkow*, Vol. XXXVI, pp. 1–276.

STECHOW, E., 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. *Zool. Jahrb. Syst.*, Bd. 42, pp. 1–172.

— 1923. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. *Zool. Jahrb. Syst.*, Bd. 47, pp. 29–270.

— 1929. Über Symbiosen von Hydroiden mit Polychaeten. *Zool. Anz.*, Bd. 86, Heft 5–6, pp. 150–3.

STRONG, L. H., 1925. Development of certain Puget Sound hydroids and medusae. *Pub. Puget Sound Biol. Stat.*, Vol. III, pp. 383–99.

TORREY, H. B., 1902. The Hydroida of the Pacific coast of North America, with especial reference to the species in the collection of the University of California. *Univ. Calif. Publ. Zool.*, Vol. I, pp. 1–104.

TOTTON, A. K., 1930. Hydroida. *Brit. Antarct.* (“*Terra Nova*”) *Exp.*, 1910, *Nat. Hist. Rep.*, Zool., Vol. V, Coelenterata, pp. 131–252.

WESTBLAD, EINAR, 1937. *Boreohydra simplex* n.gen., n.sp., ein Solitärpolyp von der norwegischen Küste. *Arch. f. Zool.*, Bd. XXIX, No. 7.

WRIGHT, T. STRETHILL, 1857. Observations on British zoophytes and on the prehensile apparatus of *Spio seticornis*. *Edinb. New Phil. Journ.*, N.S., Vol. VI.

— 1858. Observations on British zoophytes. *Edinb. New Phil. Journ.*, N.S., Vol. VII.

— 1861. Observations on British Protozoa and zoophytes. *Ann. Mag. Nat. Hist.*, Ser. 3, Vol. VIII, pp. 120–35.

— 1863. Observations on British zoophytes. *Quart. Journ. Micr. Sci.*, N.S., Vol. III, pp. 47–52.

THE SEASONAL OCCURRENCE OF MYSIDS OFF PLYMOUTH

By W. M. Tattersall, D.Sc.

University College, Cardiff

(Text-fig. 1)

In the course of his work on the plankton of the English Channel, Mr F. S. Russell (1928*b*) designed a special townet, made of stramin netting, to fish inside the Agassiz trawl as it was dragged along the bottom. The townet was so fixed as to fish a few inches above the bottom without actually stirring up bottom material. Mr Russell tells me that there was no indication that the net was catching bottom living forms, but that all the animals caught were plankton forms or animals swimming just above the bottom. The hauls, therefore, may be taken to present a picture of the fauna of the bottom layer of water, over a period of a year, and it may not be without interest to analyse the gatherings as far as mysids are concerned in an endeavour to glean information on the biology of the group.

The tow-nettings were taken at three stations in the neighbourhood of Plymouth, from June 1927 to May 1928. The three stations, referred to in the following pages as A, R, and L4, were situated as follows:

A = 2 miles east of Eddystone. Sand.
R = Off Rame Head. Mud.
L4 = Midway between the Breakwater Light and Eddystone. Mud and sand.

The Mysidacea include two groups of forms, those which are permanently planktonic and mostly oceanic, such as *Gnathophausia*, *Eucopia*, *Euchaetomera*, *Caesaromysis*, *Arachnomysis*, certain species of *Anchialina* and *Siriella*, and others, and the remainder which are normally bottom-living. It is to the latter group that the species in this collection belong. The members of this group may leave their bottom-haunting habits and undertake movements into the neighbouring water under the influence of varying stimuli and factors which may be briefly referred to.

In the first place it is almost certain that a large proportion of bottom-living forms spend part of their time in idly swimming just above the bottom. These movements are intermittent and their intensity varies with the operation of various factors in the environment. In shallow water, in suitable locations, I have often observed *Praunus flexuosus*, *P. neglectus* and *Neomysis integer* swimming about gently in 2 or 3 ft. of water in large numbers, especially on calm sunny days. The extent of their activity was seen to vary with such environmental factors as the intensity of light, the amount of water disturbance, temperature, and so on, but it was quite obvious that such idle swimming movements were a normal feature of their lives. It is not unreasonable to suppose that the majority of bottom-living forms have similar habits, and, in deeper water, where unfavourable conditions are minimized, one may suppose that idle swimming movements just above the bottom are a regular part of the normal life of the species. The fact that the present material includes fourteen out of the twenty-seven species known for the Plymouth fauna would lend support to this view, especially as the stations at which the plankton hauls were made were not suitable localities for most of the missing species, such as *Praunus flexuosus*, *P. neglectus*, *P. inermis*, *Neomysis integer* and the species of *Schistomysis*.

Mysids are also known to undergo diurnal movements in response to light intensity. Russell (1925, 1928*a*, 1931, 1933) has shown that, at Plymouth, certain mysids such as *Anchialina agilis*, *Leptomysis gracilis*, *Neomysis longicornis*, *Schistomysis*, *Erythrops* and *Gastrosaccus normani* move upwards from the bottom with the approach of darkness and may be taken at night in some numbers in mid-water. Some, such as *Anchialina agilis*, actually reach the surface in considerable numbers. I have shown (1936) that the same kind of thing happens in the waters inside the Great Barrier Reef. Fage (1933) suggests that these diurnal movements are dominated by the reproductive cycle and are more marked in the breeding season.

There is, further, evidence that in some Mysidacea at least, for example *Lophogaster typicus* (Tattersall, 1908), the breeding female becomes pelagic and rises to the surface at the time when the young are just ready to be liberated from the brood pouch, thereby ensuring the widest possible distribution for the young. A similar habit may be more generally characteristic of other species of the group, and introduces another factor which may influence movements.

Finally, Russell has called attention (1927) to the occurrence of immature mysids in plankton catches, taken in mid-water, suggesting that in the immature stages mysids are more planktonic in habit than in the adult condition.

A planktonic habit in mysids, therefore, may be either (i) permanent, or (ii) a temporary but normal and intermittent habit in the bottom-living forms, in the layers of water immediately over their haunts, varying in intensity with environmental factors such as light, wave action, temperature, and so on, or (iii) a breeding habit either during the actual processes of mating and egg laying, or to ensure a wide distribution for the young, or (iv) a habit characteristic of the immature phases.

In attempting to analyse the results of a series of tow-nettings such as the present one, it is difficult to assess the precise factor which was operating at the time of the catch or to estimate the degree to which one or more factors have combined to influence the result. Nevertheless some points of interest have emerged from this study.

THE MYSIDS AS A WHOLE

In Fig. 1 the total number of mysids caught in each tow-netting at each of the three stations has been plotted in graph form. The whole of the mysids were picked out and counted, and the figures reduced to 30 min. hauls so as to be strictly comparable.

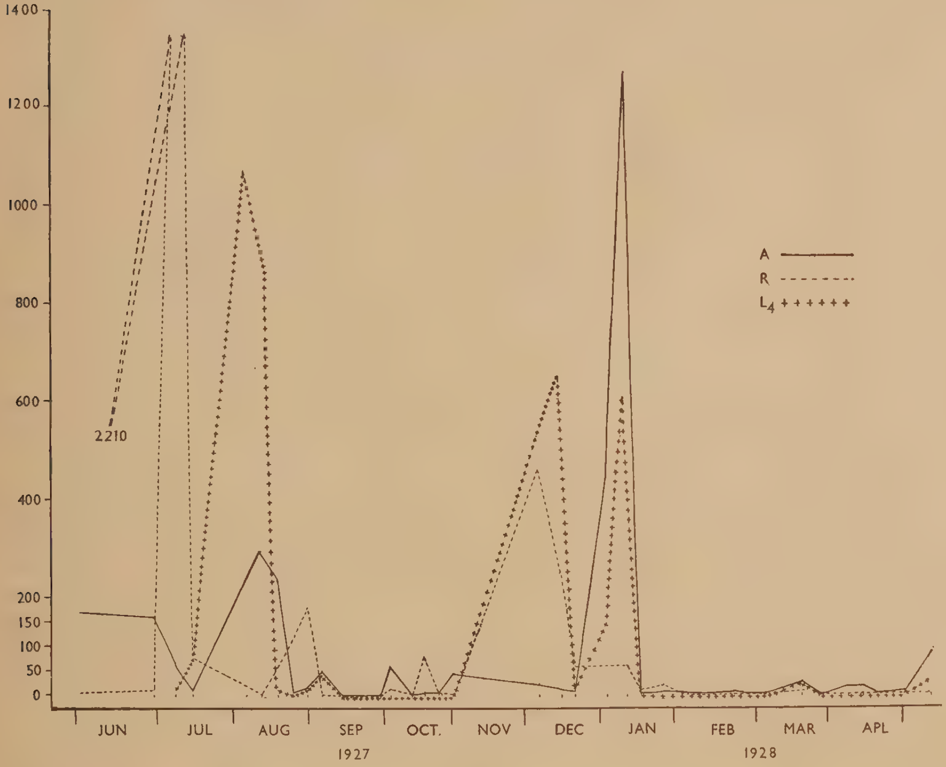


Fig. 1

From this graph it is apparent at once that, during two periods of the year, mysids appeared in the bottom plankton in very large numbers. These two periods are (i) from June to August 1927, and (ii) December 1927 and January 1928. At the other times of the year the number of mysids were small and probably represent a more or less normal picture of the idle and intermittent swimming movements of mysids in the bottom layer. The summer and winter maxima represent unusual activity for which an explanation must be sought. It is to be noted that the maxima did not always appear simultaneously at the three stations, but, taken as a whole, they are well marked.

Further analyses of the maxima show that the summer one is almost completely dominated by *Leptomysis gracilis* and that the high numbers in the catches at this period were almost entirely composed of this species. In the winter maximum, on the contrary, *L. gracilis* played a very insignificant part (negligible but for one haul of 209 specimens on 15. xii. 27) in the swarms of mysids which occurred. The dominant species was *Schistomysis ornata*, while *Anchialina agilis*, the two species of *Gastrosaccus*, and *Neomysis longicornis* also contributed considerably. The difference between the composition of the two maxima is brought out rather strikingly in Table I. In compiling this table I have selected *all* the hauls in which more than 100 specimens of mysids occurred. This is a purely arbitrary number chosen for convenience. There were sixteen such hauls, curiously enough eight in each maximum. I give the total number of mysids in each haul and the numbers of each species represented.

The occurrence of a summer maximum of *Leptomysis gracilis* is not a feature confined to the year 1927–8, but was further indicated in the year 1930 by an examination of the catches in oblique hauls above the bottom recorded by Russell (1933). Mr Russell kindly sent me the samples of the July and August hauls in that year on which the figures given in Table I of his paper are based. All the specimens submitted to me belong to *L. gracilis* except one specimen of *Neomysis longicornis*. Although these results are not strictly comparable with those of the bottom stramin net it is evident that, in 1930, *Leptomysis gracilis* was the most abundant species in the plankton in July and August, and produced a peak of the same nature, though less marked, as in the bottom catches in 1927. There is, however, much less evidence of a winter maximum in the plankton in 1930–1. On February 4 1930, 100 specimens of mysids were caught, and from November 13 1930 to April 16 1931, mysids occurred in only one haul, that on January 15 1931, when ten specimens were found.

A further difference between the two maxima must be noted. The summer maximum of *L. gracilis* is composed equally of adults of both sexes and immature forms. The precise details will be found under *L. gracilis* later in this paper, where it will be seen that, broadly speaking, immature specimens were abundant in June, and adults in July and August. Moreover, the adults were actively breeding, females with eggs or embryos in the brood pouch being present in considerable numbers. It would appear that *L. gracilis* becomes markedly planktonic during the breeding season and that the summer maximum of mysids is an expression of this reproductive activity.

On the other hand, the winter maximum of mysids was composed almost entirely of immature specimens, about half-grown or less. A few breeding females of *Schistomysis ornata*, and *Anchialina agilis*, and two breeding females of *Gastrosaccus spinifer* occurred in the winter hauls, but the number of adult specimens was very small and not at all comparable to the numbers of adult *Leptomysis gracilis* in the summer maximum. The winter maximum is obviously correlated with breeding activity among the species which compose

Table I. Composition of Mysid Fauna during Periods of Maximum Abundance

This includes the sixteen tow-nettings during the year in which the total number of mysids caught exceeded 100.

Summer maximum		Total no. of mysids	*Siriella jaltensis*	*S. clausi*	*S. armata*	*Gastrosaccus spinifer*	*G. normani*	*Anchialina agilis*	*Erythrops elegans*	*Mysidopsis angusta*	*M. gibbosa*	*Leptomysis gracilis*	*L. lingvura*	*Schistomysis ornata*	*Neomysis longicornis*
2. vi. 27	A	163	..	..	..	2	..	..	1	..	..	146	..	2	12
29. vi. 27	A	315	..	..	..	..	..	..	2	..	..	306	..	5	2
8. vii. 27	R	2210	..	..	..	..	..	9	2	..	..	2184	..	..	7
5. viii. 27	L4	1063	..	..	..	..	..	3	1	..	..	1011	..	4	44
12. viii. 27	A	294	..	..	..	..	..	..	..	..	..	284	..	3	7
	L4	885	..	..	..	..	..	2	..	1	..	875	..	2	5
19. viii. 27	A	235	..	..	..	..	1	6	1	4	3	166	..	47	7
25. viii. 27	R	108	..	..	..	..	..	2	..	..	..	94	..	6	6
Winter maximum															
6. xii. 27	R	450	2	..	..	..	2	116	1	1	2	3	1	326	1
	L4	527	..	..	..	..	7	195	6	14	7	8	..	285	5
15. xii. 27	R	233	1	..	..	..	4	6	4	3	..	1	3	209	2
	L4	643	1	..	..	18	238	30	2	3	1	209	..	56	85
3. i. 28	A	449	..	..	..	78	79	94	1	1	..	8	..	162	16
	L4	154	2	4	..	16	17	27	1	1	..	4	..	72	9
11. i. 28	A	1268	25	..	..	30	46	195	..	..	1	4	2	867	98
	L4	620	19	..	..	55	68	90	1	1	..	3	..	321	62

it, but these species do not appear to become markedly planktonic in the adult condition for breeding purposes, as does *L. gracilis*. In Table II, I have put together the data showing the months of the year in which the species dealt with in this paper are known to breed. A correlation of the data here presented with the analyses of the bottom plankton hauls will show that no other species of mysids behaves in the same way as *L. gracilis*. There is a suggestion of the same behaviour in *Schistomysis ornata* and *Anchialina agilis* but it is not nearly so definite.

TABLE II. BREEDING OF MYSIDS

Showing the months of the year in which the species dealt with in this paper have been recorded to breed. The table is compiled from data provided by the present material (T), the Plymouth Marine Fauna, 2nd edition, 1931 (P), and Colosi, 1929 for the Mediterranean (C).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Siriella armata	..	..	..	P	..	P	..	T	..	P	..	..
S. jaltensis	..	..	C	..	..	P	..	..	C	..	..	..
S. clausi	..	..	C	C	..	..	..	C	C	C	..	..
Gastrosaccus spinifer	T	..	..	..	..	..	..	..	..	..	..	..
G. normani	..	..	..	..	..	..	..	T	P	PC	..	..
Anchialina agilis	T	T	TC	..	..	P	..	C	..	TC	..	T
Erythrops elegans	..	..	..	..	..	P	..	..	..	P	..	..
Mysidopsis angusta	..	T	..	..	..	P	P	P	P	PT	..	T
M. gibbosa	..	..	..	P	..	..	P	..	..	..	T	..
Leptomysis gracilis	..	..	..	..	..	PT	T	T	T	T	..	..
L. lingvura	..	..	C	CP	C	C	C	..	C	PC	..	..
Schistomysis ornata	T	P	..	PT	T	..	..	T	T	P	..	T
Neomysis longicornis	..	..	..	..	T	PT	P	PT	P	P	P	..
Heteromysis formosa	..	..	..	..	..	..	..	..	..	P	P	..

The further question arises as to why there should be large numbers of immature forms in the bottom plankton during the winter and not at other times. Table II shows that mysids were breeding at other times of the year yet immature specimens were not conspicuously abundant in the bottom plankton hauls. In *Schistomysis ornata*, for instance, one of the dominating species of the winter maximum, adult females carrying eggs or embryos occurred in August, September and October, but there was no corresponding large number of immature forms in the bottom plankton. *Anchialina agilis* was also breeding earlier in the year without any marked accession of immature forms to the plankton. The explanation of these facts is probably to be found in an observation made by Russell (1927). He there notes the appearance of numbers of immature mysids in mid-water tow-nettings in July. This observation suggests that immature forms are more planktonic in habit than the adults, and that for the greater part of the year the young forms are to be sought for higher up in the water than the immediate bottom layer. In winter, conditions (e.g. temperature) are less favourable to a mid-water habit and the young forms are driven into deeper water and become concentrated in the bottom layer. On this assumption the winter maximum in the bottom layer would be an expression of the operation of a different set of factors from that which brings about the summer maximum. At other times of the year the young forms might be scattered over a much greater range of depth of water. Moreover, the immature forms of the spring, summer and autumn broods rapidly become adult and sink to the bottom to take up their normal bottom-haunting life. The immature forms found in winter represent the overwintering stages of the species concerned and remain in the immature or non-breeding condition for a much longer period than is customary in the summer broods. If, as it appears, immature stages are more planktonic than adults, a greater concentration of young forms is to be expected in the winter months.

The winter of 1927–8 was not abnormal in respect to its winter maximum. Mr Russell has sent me some figures for bottom plankton hauls made in 1932–3 and these show markedly high numbers for December and January. I have not examined the material but the results suggest a winter maximum of the same nature as in the winter 1927–8.

Notes on the Species of Mysids

Fourteen species in all were found in the collection, of which one, *Gastrosaccus spinifer*, has not been recorded previously from the Plymouth area, though known from other parts of Devonshire and Cornwall.

Siriella armata (M.-Ed.).

Cawsand Bay, 12. viii. 27, seven specimens including one adult ♀, carrying embryos.
A, 18. x. 27, one immature specimen.

Breeding females have been recorded from the Plymouth area in April, June and October. The occurrence of a breeding female in August fills a gap in this series and suggests that the species has a continuous breeding period at Plymouth lasting at least from April to October. This does not agree with the results of Fage's work at Concarneau where he found that the breeding period of the species extended from September to March.

Siriella jaltensis Czern.

6. xii. 27, R, 2 juv.: 15. xii. 27, R, 1 juv.; L4, 1 juv.: 21. xii. 27, R, 1 ♂: 3. i. 28, A, 3 ♂, 4 juv.; L4, 2 juv.: 11. i. 28, A, 7 ♂, 2 ♀, 16 juv.; R, 2 juv.; L4, 6 ♂, 13 ♀: 26. i. 28, R, 1 ♂, 1 ♀; L4, 1 ♂.

The species only occurred during the time of the winter maximum and then only in small numbers. No breeding specimens were found and none of the specimens is fully mature. This material throws no new light on the breeding season. The only Plymouth records of the breeding season refer to specimens caught in June. Fage (1933) gives the early spring, March and April, and the late summer, August and September, as the breeding times of this species at Concarneau. The only Plymouth record is just midway between these two periods.

Siriella clausi G. O. Sars.

3. i. 28, A, 1 adult ♀; L4, 1 adult ♂, 3 juv.: 17. i. 28, R, 4 juv.; L4, 3 juv.

None of the specimens is breeding and all but two are immature. The species was only met with during the winter maximum. There are no records of breeding females for Plymouth. Fage (1933) gives the same breeding season at Concarneau for this species as for *S. jaltensis*.

Gastrosaccus spinifer (Goës).

2. vi. 27, A, 2 juv.: 15. xii. 27, L4, 18 juv.: 21. xii. 27, A, 1 juv.: 3. i. 28, A, 2 ♀, 78 juv.; L4, 16 juv.: 11. i. 28, A, 30 juv.; R, 5 juv.; L4, 1 ♂, 1 ♀, 51 juv.: 30. iv. 28, A, 1 juv.

This species is new to the Plymouth fauna. It has, however, been recorded from Starcross, the mouth of the R. Exe, and Padstow (Norman & Scott, 1906). The two females caught at St. A in January were carrying eggs in the brood pouch. Fage (1933) states that at Concarneau breeding females were found from February to May.

Gastrosaccus normani (G. O. Sars).

	A			R			L4		
	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.
15. vii. 27	..	..	..	..	..	..	..	..	1
19. viii. 27	..	1	..	..	..	..	..	..	..
6. ix. 27	..	1	1	..	..	..	..	..	..
4. x. 27	2	1	..	..	..	..	..	..	..
1. xi. 27	..	..	1	..	..	..	..	..	..
6. xii. 27	..	..	2	..	..	2	..	..	7
15 xii. 27	..	..	2	..	..	4	..	..	238
21. xii. 27	..	..	3	..	..	2	..	..	..
3. i. 28	..	..	79	..	..	..	..	..	17
11. i. 28	..	..	46	..	..	8	..	..	68
26. i. 28	..	..	..	4	4	..	..	..	..
23. iii. 28	..	..	..	1	..	..	..	..	..

Only one female carrying eggs appears in the collection and that was taken at St. A in August. Fage (1933) notes that the species is more abundant in the night plankton from the end of the summer to the end of the autumn and that this is its breeding season. In the present collection large numbers of immature specimens appeared in the bottom plankton in December and January. Previous Plymouth records show that breeding females have been found in September and October. The Plymouth observations, therefore, support Fage's conclusions that the summer and autumn are the breeding season for this species. The large number of immature specimens found in December and January represent the last of the autumn broods which are over-wintering in the immature condition and will probably breed early in the spring.

One further point should be mentioned. Some of the specimens caught on January 11 and all those caught on January 26 and March 23 1928, had forwardly directed lobes on the carapace exactly as is found in *G. sanctus*, but the pleopods of the males of such lobed specimens were clearly of the *G. normani* type. I have already called attention (1908) to the occurrence of lobed specimens captured by the "Huxley" in the Bay of Biscay in August 1906. I have never been able to solve this problem, but it does appear that the presence or absence of such lobes on the carapace is not infallible as a specific character.

Anchialina agilis (G. O. Sars).

	A			R			L4		
	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.
8. vii. 27	..	..	..	..	..	18	..	..	..
5. viii. 27	..	..	..	..	..	..	3	..	..
12. viii. 27	..	..	..	..	..	..	2	..	..
19. viii. 27	2	4	..	..	..	..	..	..	..
25. viii. 27	..	..	..	1	1	..	1	..	..
31. viii. 27	..	..	..	4	1	..	..	..	..
6. ix. 27	..	2	..	..	..	..	..	..	..
15. ix. 27	..	..	..	1	..	..	..	..	..
4. x. 27	2	1	..	..	2	..	..	..	..
18. x. 27	2	..	..	..	..	..	..	..	..
25. x. 27	1	..	..	..	..	..	..	..	..
1. xi. 27	7	5	7	..	..	..	..	..	..
6. xii. 27	..	..	14	20	5	91	23	28	144
15. xii. 27	..	..	—	..	1	5	..	1	29
21. xii. 27	..	..	—	2	4	25	..	..	5
3. i. 28	21	24	51	..	..	..	3	2	22
11. i. 28	18	17	160	..	..	11	9	17	64
17. i. 28	..	..	..	..	1	3	..	..	..
26. i. 28	..	..	1	1	..	..	..	1	..
24. ii. 28	..	..	3	..	..	..	..	..	..
23. iii. 28	4	1	..	2	..	..	..	1	..

This species occurred sparingly in the adult condition during most of the year, but in December 1927 and January 1928 large numbers of immature specimens, accompanied by a good many adults contributed to the winter maximum. Breeding females occurred in October and December 1927, and January, February and March 1928. The large number of immature specimens in the winter is clearly correlated with active reproduction during the winter months. The increased number of adults in the winter also suggests that *Anchialina agilis*, like *Leptomysis gracilis*, becomes more planktonic and active in its movements during the breeding season. This reproductive planktonic phase in the adult is not so marked as in *L. gracilis*, but is perhaps more emphatic than in *Schistomysis ornata*. Other Plymouth records show that breeding females have been taken there in June. None of the specimens caught between July and October 1927 were actually carrying eggs or embryos, though some of them looked as if they had recently shed their brood.

Erythrops elegans (G. O. Sars).

2. vi. 27, A, 1 ♀; R, 1 ♂: 29. vi. 27, A, 2 ♀: 8. vii. 27, R, 3 ♀: 5. viii. 27, L4, 1 ♂: 19. viii. 27, A, 1 ♂: 18. x. 27, A, 1 ♀; R, 1 ♂: 1. xi. 27, A, 1 ♂: 6. xii. 27, R, 1 ♂; L4, 1 ♂, 5 ♀: 15. xii. 27, R, 1 ♂, 3 ♀; L4, 2 juv.: 3. i. 28, A, 1 ♂; L4, 1 ♀: 11. i. 28, L4, 1 ♀: 23. iii. 28, A, 2 ♀: 18. iv. 28, A, 2 ♂, 2 juv.

No breeding females occurred in the plankton, and the species made no contribution either to the summer or winter maximum.

Mysidopsis angusta G. O. Sars.

2. vi. 27, R, 1 ♂: 12. viii. 27, L4, 1 ♂: 19. viii. 27, A, 2 ♂, 2 ♀: 4. x. 27, A, 2 ♂, 1 ♀: 18. x. 27, A, 1 ♀: 25. x. 27, A, 1 ♂: 1. xi. 27, A, 1 ♂: 6. xii. 27, R, 1 ♂; L4, 3 ♂, 4 ♀, 7 juv.: 15. xii. 27, R, 1 ♂, 1 ♀, 1 juv.; L4, 1 ♂, 2 juv.: 21. xii. 27, R, 1 ♀, 4 juv.; L4, 1 juv.: 3. i. 28, A, 1 ♀; L4, 1 ♂: 11. i. 28, L4, 1 juv.: 23. ii. 28, A, 2 ♀: 23. iii. 28, L4, 2 ♂, 1 ♀: 23. iv. 28, A, 1 ♂; L4, 1 juv.: 30. iv. 28, A, 1 juv.: 11. v. 28, A, 1 ♀.

Breeding females occurred in October, December and February. The Plymouth records show a more or less continuous breeding season from June to February. The species contributes nothing to either the summer or winter maximum, but occurs as isolated specimens or in very small numbers all the year round in the bottom plankton.

Mysidopsis gibbosa G. O. Sars.

19. viii. 27, A, 3 ♀: 1. xi. 27, A, 1 ♀: 6. xii. 27, R, 2 juv.; L4, 1 juv.: 15. xii. 27, L4, 1 juv.: 11. i. 28, A, 1 ♀: 23. ii. 28, A, 1 ♂, 1 ♀.

The single specimen caught on November 1 1927, was a breeding female with embryos. Previous Plymouth records refer to breeding females caught in April and July. This suggests that the species has a continuous breeding season extending from April to November. The species is apparently a casual member of the bottom plankton fauna.

Leptomysis gracilis (G. O. Sars).

	A			R			L4		
	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.
2. vi. 27	70	60	16	2	..	3	..	..	..
29. vi. 27	14	26	266	1	..	19	..	..	..
8. vii. 27	12	9	38	2180 (not sexed)			6	2	9
15. vii. 27	..	..	15	13	6	7	4	1	60
5. viii. 27	..	..	..	..	..	..	467	544	..
12. viii. 27	163	121	..	..	2	..	415	460	..
19. viii. 27	50	116	..	25	26	..	4	6	..
25. viii. 27	1	..	5	36	58	..	..	..	..
31. viii. 27	4	1	..	42	44	..	..	..	..
6. ix. 27	21	20	..	..	..	..	22	20	..
15. ix. 27	..	..	..	..	..	..	..	1	..
4. x. 27	28	15	3	5	1	..	2	..	1
18. x. 27	..	..	2	4	4	..	..	..	..
25. x. 27	2	..	..	..	..	..	..	..	..
1. xi. 27	4	5	..	2	..	..	..	..	..
6. xii. 27	..	..	2	..	..	3	2	..	6
15. xii. 27	..	..	7	..	..	1	..	1	208
21. xii. 27	..	..	..	..	..	2	..	..	..
3. i. 28	7	1	..	..	..	..	..	..	4
11. i. 28	..	..	4	..	..	8	1	..	2
17. i. 28	..	..	..	..	..	..	1	..	..
14. ii. 28	..	1	..	..	..	..	1	1	..
24. ii. 28	1	..	..	..	..	..	..	..	..
23. iii. 28	..	..	2	..	..	..	..	3	..
12. iv. 28	..	..	14	..	..	..	..	..	..
18. iv. 28	..	1	1	..	..	1	1	1	..
23. iv. 28	..	..	..	..	..	..	..	3	..
30. iv. 28	..	..	..	..	1	1	1	..	..
11. v. 28	25	55	..	..	..	..	11	13	..

This species is entirely responsible for the summer maximum of mysids in the bottom layer of water. Plymouth records, based mainly on the evidence of this collection, show that the species is actively breeding from June to October, females carrying eggs or embryos appearing in considerable numbers throughout that period. No breeding females were found after October and the numbers of specimens of the species in the bottom layers fell considerably for the remainder of the year from November to May. The only exception occurred on December 15 1927 at L4, when 208 immature specimens were caught. Adults again became numerous in the plankton in May and indicate that the species was again preparing for the breeding season.

The present material seems to suggest that *L. gracilis* becomes very active in the adult breeding condition, and leaves the actual bottom for a planktonic life at that time. They remain, however, in the bottom layer of water and here the young are liberated. It will be noticed from the table that during the breeding season the number of immature specimens in the bottom layer is not very large. The evidence supplied by Russell (1927) suggests that the immature forms at this time are to be found in the higher layers of water, about midway between the surface and bottom. In the winter months the immature stages are driven into deeper water, and the occurrence of 208 specimens at L4 in December 1927 seems to be explained on these grounds. In other words the depth position of the larvae in the plankton is influenced by environmental factors, probably by the temperature of the water.

This species therefore provides evidence of two types of movement, (i) a movement from a bottom living to a planktonic life in the adult condition for breeding purposes, and (ii) a migration of the immature forms to greater or lesser depths according to the season of the year, movements which are presumably influenced by temperature.

Leptomysis lingvura (G. O. Sars).

1. xi. 27, A, 1 ♂: 6. xii. 27, R, 1 juv.: 15. xii. 27, R, 3 juv.: 21. xii. 27, A, 2 juv.; R, 1 juv.: 11. i. 28, A, 2 juv.: 23. iii. 28, A, 1 juv.

All the specimens but one are immature and no breeding females were taken. Plymouth records refer to breeding females caught in April and October, but in the Mediterranean the breeding season appears to be a continuous one from March to October (Colosi, 1929).

Schistomysis ornata (G. O. Sars).

	A			R			L4		
	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.
2. vi. 27	..	..	2	..	..	..	..	..	..
29. vi. 27	1	2	2	..	..	..	..	..	..
5. viii. 27	..	..	..	..	..	..	1	..	3
12. viii. 27	1	1	1	..	..	..	..	..	..
19. viii. 27	18	23	6	1	1	..	..	..	..
25. viii. 27	..	1	..	1	3	2	..	..	..

Schistomysis ornata (G. O. Sars) (*cont.*)

	A			R			L4		
31. viii. 27	6	1	..	..	..	..	..	..	..
30. ix. 27	..	..	..	..	1	..	..	..	..
4. x. 27	1	1	4	1	2	..	..	..	..
18. x. 27	..	..	..	1	3	2	..	..	..
1. xi. 27	2	3	9	..	..	..	..	..	1
6. xii. 27	..	..	1	..	..	326	..	..	285
15. xii. 27	..	..	1	8	17	184	1	1	54
21. xii. 27	..	..	..	1	3	6	1	..	..
3. i. 28	..	1	161	..	..	..	..	2	70
11. i. 28	..	..	867	..	..	20	..	..	321
26. i. 28	..	1	..	4	3	..	..	..	..
3. ii. 28	..	..	..	..	..	2	..	..	..
29. ii. 28	..	..	..	..	..	..	..	2	..
23. iii. 28	2	1	2	..	1	..	3	3	7
12. iv. 28	..	1	..	..	..	..	..	..	..
18. iv. 28	1	1	8	..	..	..	..	..	..
23. iv. 28	..	..	1	..	..	..	..	..	..
11. v. 28	..	1	1	..	..	..	..	..	..

The numbers of adult specimens in the bottom layer of water was never very large and may, for the most part, be accounted for as the result of a normal habit of swimming about idly near their bottom haunts. There is a faint suggestion that when breeding these movements are more marked, for on August 19 1927, when forty-one adults were caught at St. A, and on December 15 1927, when twenty-five adults were caught at St. R, the females in both hauls were carrying eggs or embryos. Such breeding movements are not nearly so well marked and definite as in *Leptomysis gracilis*, or in *Anchialina agilis*. On the other hand, immature specimens were largely responsible for the winter maximum of mysids in the bottom layer of water. The evidence from adult specimens shows that there was considerable breeding activity during December and January. From Table II, however, this species would appear to be breeding practically all the year round. In the present material breeding females occurred in January, April, May, August, September and December, and other Plymouth records show that breeding females have occurred in February and October. The question naturally arises as to what happens to the immature forms at other seasons of the year except the winter. The table of the occurrence of this species during 1927–8 shows no marked accession of immature forms to the bottom plankton at these times and there is no other evidence available. Russell (1927) does not mention this species when observing that immature mysids are to be found in mid-water hauls in considerable numbers. His remarks refer mainly to *Leptomysis gracilis*. It is possible, however, that at seasons of the year, other than winter, the immature forms may inhabit layers of water higher up than the bottom layer and that this may account for their absence in the bottom water at times other than winter when the adults are actively breeding.

To sum up, *Schistomysis ornata* does show some slight movements from its bottom living haunts to the bottom water for breeding purposes, but the movement is not nearly so marked or so definite as in *Leptomysis gracilis*. Large numbers of immature forms occur in the bottom layer of the plankton in the winter, but there is no evidence of what happens to these immature forms at other seasons of the year.

Neomysis longicornis (M.-Ed.).

	A			R			L4		
	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.
2. vi. 27	6	4	2	..	..	..	..	..	..
29. vi. 27	1	1	..	..	..	..	..	..	..
8. vii. 27	..	..	..	8	6	..	..	..	..
15. vii. 27	1	1	..	..	..	..	..	..	..
5. viii. 27	..	..	..	..	..	..	15	29	..
12. viii. 27	6	1	..	..	..	..	1	2	1
19. viii. 27	5	1	1	4	2	..	..	..	..
25. viii. 27	..	..	..	4	2	..	..	..	..
31. viii. 27	2	2	1	..	..	..	..	..	..
6. ix. 27	6	..	..	..	..	..	..	..	..
4. x. 27	..	1	..	..	..	..	..	..	..
6. xii. 27	..	..	..	..	1	..	..	5	..
15. xii. 27	..	..	..	1	..	1	5	1	79
3. i. 28	6	2	8	..	..	..	6	1	2
11. i. 28	21	19	48	..	..	..	29	34	4
24. ii. 28	..	3	..	..	..	..	..	..	..
23. iii. 28	..	..	..	1	..	..	..	..	..
11. v. 28	..	3	..	..	..	..	..	..	..

This species appears to behave very much as *Schistomysis ornata*. It occurred in small numbers fairly regularly throughout the year. Breeding females were captured in May, June and August, and the Plymouth records indicate a continuous period of breeding activity from May to November. The species took part in the winter maximum of mysids, there being a small accession of immature and young forms to the bottom layer of water in December and January.

Heteromysis formosa S. J. Smith.

23. iii. 28, L4, 1 adult ♂.

SUMMARY

An analysis is made of the mysids which occurred in a series of bottom stramin net plankton hauls made at three stations in the Plymouth area in 1927–8.

There were two marked maxima in numbers of mysids, a summer one in July and August, and a winter one in December and January.

The summer maximum was due entirely to *Leptomysis gracilis*.

The winter maximum was due mainly to *Schistomysis ornata* and *Anchialina agilis*, but the two species of *Gastrosaccus*, and *Neomysis longicornis* also contributed to a lesser degree.

The summer maximum was composed mainly of adult males and breeding females of *Leptomysis gracilis* which appear to become markedly planktonic in habit at the breeding season though keeping to the deeper layers. Immature specimens were present but the majority were probably higher up in the water (mid-water).

There is a suggestion that a similar planktonic habit is to be found in *Schistomysis ornata* and *Anchialina agilis* during their breeding period in the winter, but it is not nearly so marked as in *Leptomysis gracilis*.

The winter maximum is mainly due to large numbers of immature forms and it is suggested that environmental factors, probably temperature, cause a concentration of immature stages in the bottom water during winter. At other times of the year these immature forms are distributed over a much greater depth range of water.

Idle swimming movements just over the bottom are a normal habit of bottom living mysids.

The collection provides evidence of three types of movements in mysids: (i) idle swimming just over the bottom, (ii) definite and marked movements into the plankton in the adult condition during the breeding season, and (iii) movements of the immature forms to greater or lesser depths according to environmental conditions, probably temperature.

REFERENCES

COLOSI, G., 1929. I Misidacei del Golfo di Napoli. *Pub. Stat. Zool. Nap.*, Vol. IX, fasc. 3, pp. 405–41.

FAGE, L., 1933. Pêches planctoniques à la lumière effectuées à Banyulis-sur-Mer et à Concarneau. III. Crustacés. *Arch. Zool. Expér. Gén.*, Tome 76, pp. 105–248.

NORMAN, A. M. & SCOTT, A., 1906. *The Crustacea of Devon and Cornwall.* London.

RUSSELL, F. S., 1925. The vertical distribution of marine macroplankton. I. An observation on diurnal changes. *Journ. Mar. Biol. Assoc.*, Vol. XIII, pp. 769–809.

—— 1927. *Ibid.* V. The distribution of animals caught in the ring trawl in the daytime in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XIV, pp. 557–608.

—— 1928*a*. *Ibid.* VI. Further observations on diurnal changes. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 81–104.

—— 1928*b*. A net for catching plankton near the bottom. *Journ. Mar. Biol. Assoc.* Vol. XV, pp. 105–8.

—— 1931. The vertical distribution of marine macroplankton. XI. Further observations on diurnal changes. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 767–84.

—— 1933. The seasonal distribution of macroplankton as shown by catches in the 2-metre stramin ring trawl in offshore waters off Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 73–82.

TATTERSALL, W. M., 1908. The Schizopoda and Isopoda collected by the "Huxley" from the north side of the Bay of Biscay in August 1906. *Journ. Mar. Biol. Assoc.*, Vol. VII, pp. 189–96.

—— 1936. The Zooplankton. V. The occurrence and seasonal distribution of the Mysidacea and Euphausiacea. *Great Barrier Reef Exped.* 1928–29. *Sci. Rep.* (*Brit. Mus.*), Vol. II, No. 8, pp. 277–89.

THE BIOLOGY OF *PURPURA LAPILLUS*. PART II. GROWTH

By Hilary B. Moore, Ph.D.
Bermuda Biological Station, Bermuda

(Text-figs. 1–6)

In a previous paper (Moore, 1936) an account was given of certain variations in the shape and colour of the shell in *Purpura*, and it was pointed out that these variations are apparently controlled by diet. It was shown that growth ceases at the onset of sexual maturity, and at the same time other changes such as the thickening of the edge of the shell take place. It was shown also that both the proportion of the population exhibiting these changes, and the average size at which they occur, vary considerably from one locality to another, this variation also being apparently correlated with the nature of the animal's diet. The present paper consists of a study of the growth of the shell and soft parts and an attempt to show whether the observed differences in size at sexual maturity in different populations are to be accounted for by differences in the growth rate during the growing phase.

The growth rate of this species is difficult to determine for several reasons. In the first place, as will be shown later (Moore, 1938, p. 67), the young and the adults live in different habitats, thus rendering it impossible to obtain a representative sample of the whole population. Even were this possible, the animal breeds throughout the year, so that its size distribution does not show year groups from which growth can be determined. I was therefore forced to use a method of marking individual shells, which involved the marking of large numbers, their release on the shore, and the subsequent recapture at intervals of the small proportion which could be found. If a true picture is to be obtained of growth under normal conditions it is essential that the growth period under observation should be passed in the natural habitat on the shore; but the very small shells could not be found again after they had been marked, and the difficulties of marking them were considerable. In practice therefore it was found necessary to determine the growth of the very small sizes in a laboratory tank, and to assume that the results so obtained were at any rate some indication of what the growth would have been under normal conditions. By linking these figures with those for larger animals living under natural conditions on the shore an approximate picture of the total growth of the animal has been obtained.

The young *Purpura* were obtained from egg capsules brought in from the shore when on the point of hatching, or, on one occasion, from eggs laid in a tank in the laboratory. They were kept in sea water in finger bowls until they hatched, when they were transferred to stones well covered with the polychaete *Spirorbis borealis* and free from algae and sponges. The stones were placed in a tank in which tides consisting of $8\frac{1}{4}$ hr. immersion and $4\frac{1}{4}$ hr. emersion were maintained electrically, and the tank was screened from too bright light to avoid excessive algal growth. The young *Purpura* lived well in such a habitat on a diet of *Spirorbis*, and showed little tendency to climb out of the water as they do when no tide is supplied. It was found, however, that the duration of the tide was of little consequence so long as the animals were uncovered at intervals. In addition to the above experiments, a few very small *Purpura* were brought in from the shore and their shells painted with cellulose paint, so that new growth appeared as clean shell. As there was a suggestion of a normal change of diet with increasing size (see Moore, 1938, p. 67), some stones covered with small *Balanus balanoides* were included as an alternative diet.

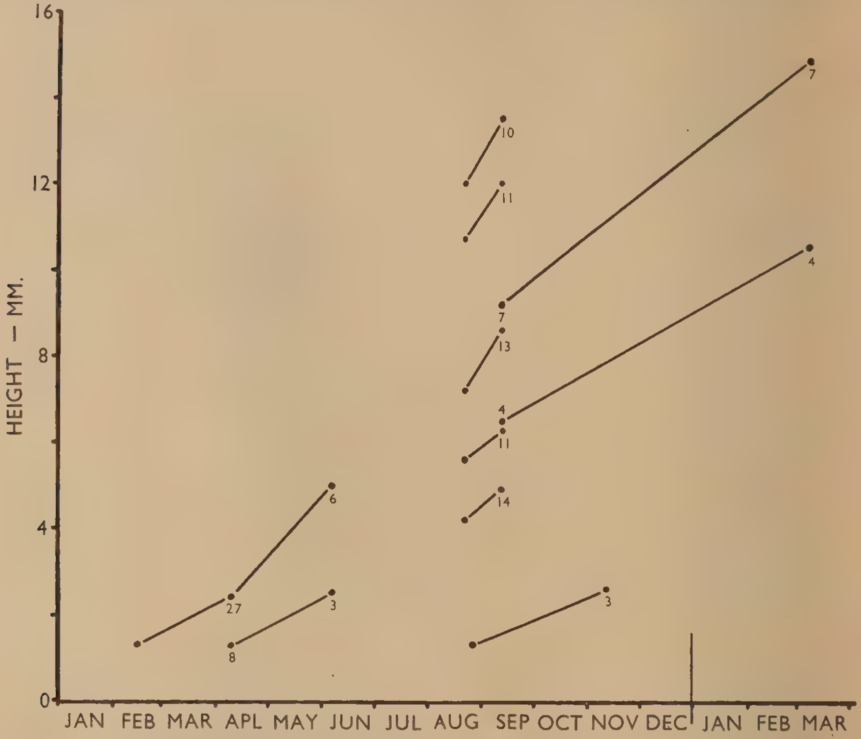


Fig. 1. Growth of batches of young *Purpura* in a tidal tank at Plymouth. Figures indicate numbers of individuals. Height at hatching approximately 1·3 mm.

The results from these experiments are brought together in Fig. 1. The series is incomplete, and the numbers of individuals are small, but the results may at least be taken as suggesting a growth of from 10 to 15 mm. in the first year. Laboratory conditions are probably very much closer to normal for these small *Purpura*, which live in sheltered crevices and under stones, than they would be for the larger animals which live in the open, and whose feeding is more dependent on weather conditions. Colton (1916) has attempted to estimate the growth of this species at Mount Desert Island from the number of rings on the shell, believing that these rings are formed each winter. He adduces no evidence to prove this, and as he makes no mention of the important matter of cessation of growth at sexual maturity, his results must remain open to doubt. If, however, his assumptions are correct, his figure of 11–15 mm. high at the first winter is comparable with the results obtained at Plymouth.

Drake's Island, in Plymouth Sound, was used for the main field experiments on the growth of the larger sizes. The method of marking was similar to that described for *Littorina littorea* (Moore, 1937, p. 723), the lip of the shell being notched with a carborundum wheel, and the apex of the shell dipped in cellulose paint. In September 1934, 2745 such marked shells were released on Drake's Island, on the same spot from which they were collected. Of these, the sex of 995 was determined and indicated by a different colour of paint, but as no difference of growth rate was found in the two sexes, and as it was later realized that growth occurs only while the animal is sexually immature, it was decided to combine the results from all the marked animals. The living shells were recaptured at intervals and taken back to the laboratory for measurement of growth. During this process, care was taken to keep them cool, and they were returned to the shore as soon as possible, either the same or the next day. The numbers of growing shells recaptured, together with the amounts of growth, are shown in Fig. 2. This figure also shows the results for a further 1500 shells which were released in May 1935 a short way from the first group, the numbers of the first group recaptured having by then dropped to so low a figure as to necessitate replacements.

The method of calculating the amount of increase in height of a shell corresponding to an observed increment to the lip has already been described for *Littorina littorea* (Moore, 1937, p. 727), and is applicable in the same way to *Purpura* once the necessary constants and their variation with size of shell have been determined for the population in question. The shells, when brought in to the laboratory, were sorted into millimetre groups according to their height, and the increment to the lip of the shell measured for each individual. From these figures the mean increment of height, and hence the mean initial height at marking, were determined for each group. Owing to the gap between the last measurement of the first group of animals on March 27, and the release of the second group on May 8, it was necessary to calculate what the growth would have been during that period on the assumption that the rate was the same as during the previous period of January 9 to March 27, the value so obtained being then used as a base line for the growth of the second group.

Although only growing, thin type, shells were used for the growth experiments, it is probable that the cessation of growth at the onset of sexual maturity is not instantaneous, so that at any rate some of the decrease in growth rate of the largest sizes is to be accounted for in this way. If we assume a height for the young shells of 10–15 mm. at the end of their first year, then they will grow about another 11 mm. in their second year, and a slightly smaller growth rate in their third year would bring them to sexual maturity (at a mean size of 29·5 mm. for this population) at from 2½ to 3 years old. The error due to abnormal conditions in the young stages is unlikely to be more than ±6 months at the outside.

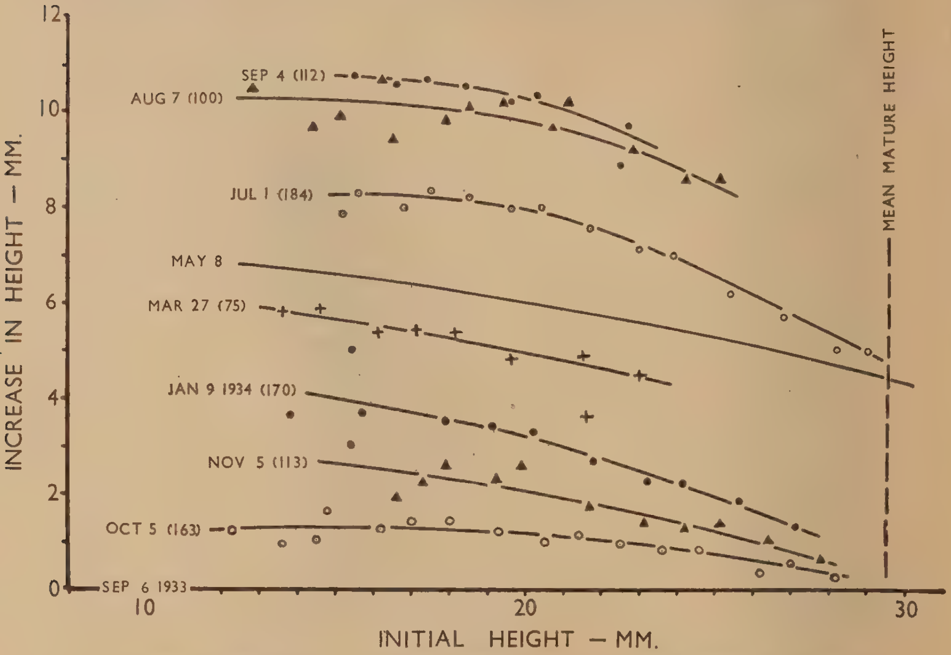


Fig. 2. Curves, at intervals up to one year, relating growth of large *Purpura* on the shore at Drake's Island, to initial height of shell. Each point represents the mean for a group of animals, and the total number for each curve is shown in brackets.

A small number of results are available also from shells kept on the shore at Port Erin, in the Isle of Man (Fig. 3); consecutive measurements of height were obtained from individual animals which had been marked with serially numbered silver tags wired to the lip of the shell. No data are available here for the growth rate of the young shells, but for the larger ones the average growth seems to be about 8–10 mm. per year. These curves show clearly the cessation of growth of the shell at sexual maturity. Colton's figures show an increase of two to five millimetres in height per year after the first year, but this may have included maturing or mature animals. Growth data for a short period during the summer from a number of localities in Devon and Cornwall (see below) show a growth of 0·5–4 mm. per hundred days, the localities having been chosen to represent extremes of certain environmental characters.

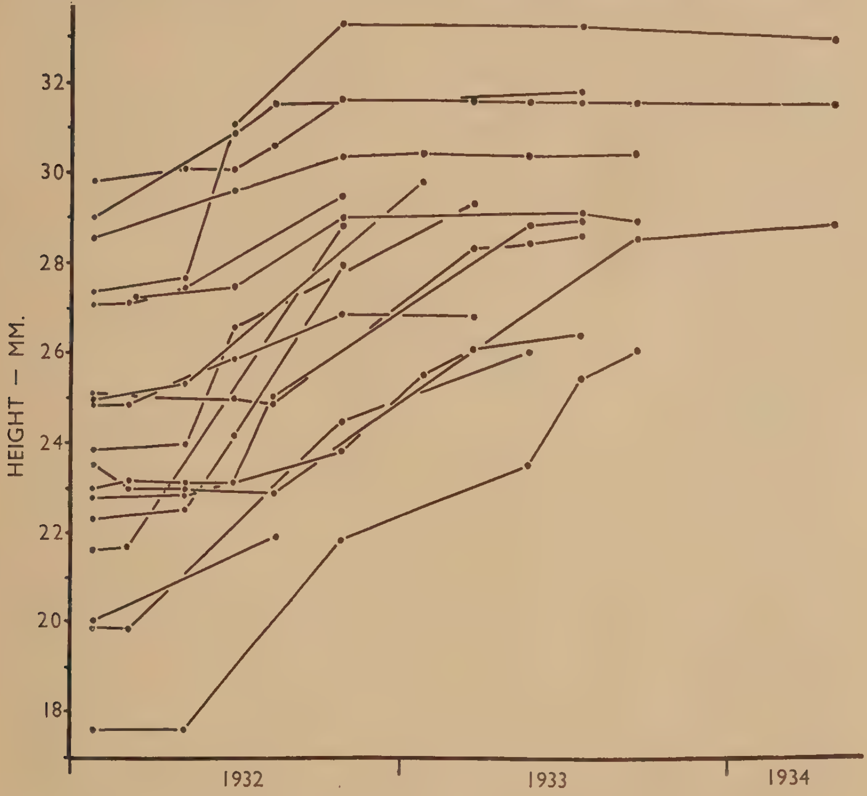


Fig. 3. Growth of individual *Purpura* on the shore at Port Erin, Isle of Man.

In comparing populations of *Purpura* from different localities, it was found (Moore, 1936) that there was a definite tendency for those which had fed on a diet of *Mytilus edulis*, in contradistinction to one of barnacles, to attain sexual maturity, with cessation of shell growth, at a greater size, but for there to be a smaller proportion of the mature, non-growing phase in the population. The percentage of these non-growing shells varied from 0 to 98 %, which seemed too wide a range to be accounted for by hastening or delay of maturity unless this were correlated with a considerable variation in growth rate. In the hope of testing the latter point, samples were taken in the summers of 1935 and

1936 from various selected localities in the west of England, marked in the usual way, and released in the places from which they were collected. After approximately three months these animals were recaptured, and the amounts of new shell growth measured. To obtain an adequate picture of the local growth conditions it would be essential to know the growth rate of all sizes of shells, but it was clearly impossible in the time available to deal with any but the larger sizes which could be found again on the shore. It would also have been desirable to work a larger number of localities, but the labour involved would have been too great. The principal characteristics of the populations and localities are shown in Table I. The localities are shown in the maps in my paper of 1936, where fuller details of the other characteristics are also given. The mean thick type height is the height at sexual maturity; the wave-exposure scale ranges from 0 = complete shelter, to 100 = exposure to all winds from all quarters; the abundance of *Mytilus* ranges from 0 = absent to ++++ = very abundant.

TABLE I

Locality	Mean thick type height (mm.)	Percentage of thick type in population	Wave exposure	Abundance of *Mytilus*
Porthcurno	18·9	88·6	9	0
Wanson Mouth	19·9	89·7	55	+
Bedruthan Steps	24·6	6·9	51	++++
Trebarwith Sands	27·0	4·0	12	++++
Salthouse	27·4	92·6	54	++++
Biddle Head, Salcombe	28·7	81·8	6	0
Duckpool	29·4	3·6	45	++++
Drake's Island	29·5	54·7	0	++

The results obtained are shown in Fig. 4, and unfortunately they are inconclusive so far as the original problem is concerned. It is true that the *Purpura* from Biddle Head, Salcombe, which attain the large size at maturity of 28·7 mm., also show the highest growth rate, while Wanson Mouth with the lowest growth rate shows the small size at maturity of 19·9 mm. It is possible that this is significant, but the localities with intermediate mature heights show very varying growth rates, and Porthcurno, which attains an even smaller height at maturity than Wanson Mouth, has not nearly so low a growth rate, at least in the sizes used in the experiment. More detailed experiments would be necessary to clear up these points, but certain facts of value emerge from the experiments. In the first place the rates of growth in different localities are very different. Individuals of two centimetres high from Salcombe, for example, grow at ten times the rate of those of similar height from Wanson Mouth. The other noteworthy point is the lack of constancy in the relation of growth rate to size of shell, some populations increasing in growth rate with increasing size while others decrease. This is perhaps to be accounted for by variations in the relative values of the food supply in the young, *Spirorbis*-fed, stages, and the older, *Mytilus*- or barnacle-fed, stages in the different localities.

The seasonal variation in tissue weight was determined in material from Misery Point, at the mouth of the river Yealm. Samples of the thick and thin types were taken at intervals and sorted into millimetre groups. Twenty individuals from each group were then dropped into boiling water for a minute, removed from their shells, and both animals and shells dried to a constant weight in a boiling water oven. The question of shell weight was dealt with in a previous paper, and it was found that it showed no seasonal variation. In

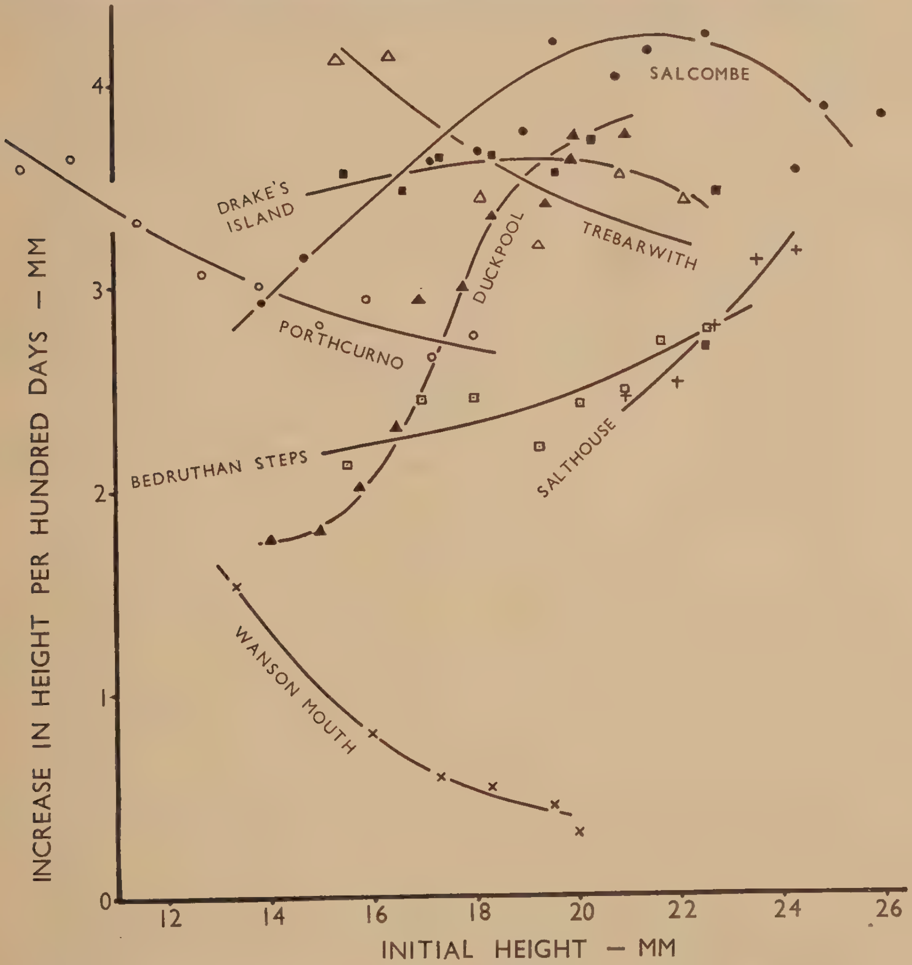


Fig. 4. The relation of growth to initial height in *Purpura* from different localities for a short period during the summer.

the thin-shelled immature animals, no significant seasonal variation in the tissue weight was found either, but the mature animals showed a considerable variation. Fig. 5 shows the seasonal changes in tissue weight of a *Purpura* 25·5 mm. in height, which is the mean size for mature shells for this locality. As will be seen, the tissue weight drops rapidly from October to the beginning of April, and then rises again up to July, when observations ceased. This drop in weight may be caused by spawning, or by inability of the animal to obtain adequate nourishment during the winter months when the weather is too stormy for it to come out onto the open rocks to obtain its food. This latter explanation is unlikely, however, as the locality is well sheltered from the open sea, and no such winter drop in weight is shown by the larger immature animals feeding on the same diet and side by side with those that were mature. Yet another possibility is that the drop in weight is not directly due to the loss of ova or sperm, but to cessation of feeding during the period when the

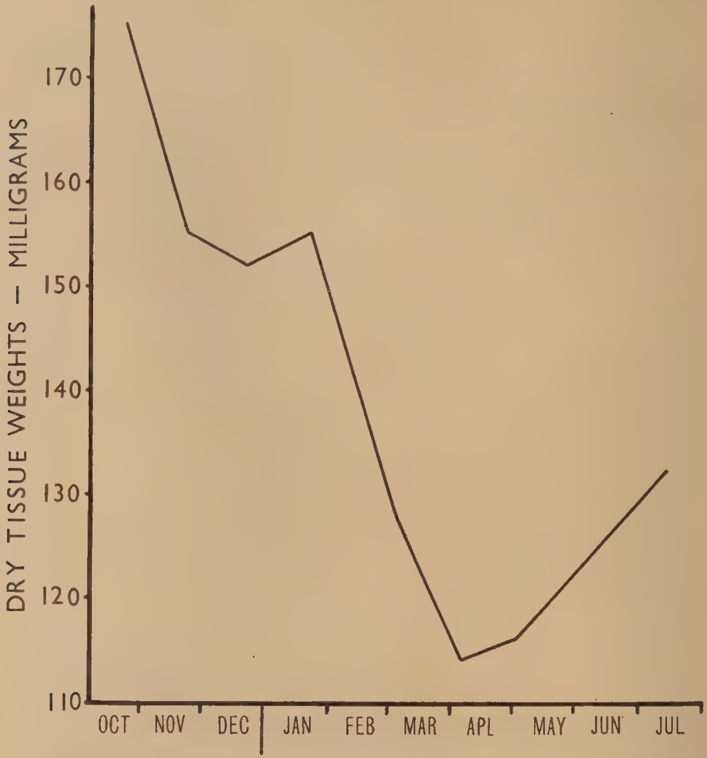


Fig. 5. Seasonal variation in tissue weight of mature (non-growing) *Purpura*, 25·5 mm. high, at Misery Point, Yealm.

animals congregate in crevices to deposit their eggs. In any case, however, the drop in weight appears to be associated in some way with spawning. Pelseneer (1935, p. 445) quotes Peach as giving January to April as the principal spawning season of this species, and Garstang as giving January to April and September. Colton (1916) says that the young are hatched throughout the greater part of the summer, but most in August, and, allowing for their taking four months to hatch, as stated by Pelseneer (1935, p. 527), they would have been laid about April. In the Plymouth neighbourhood, although egg capsules are to be found throughout the year, they seem to be most abundant in the early summer, and the tissue weight curves suggest that the main spawning period is during the winter and spring.

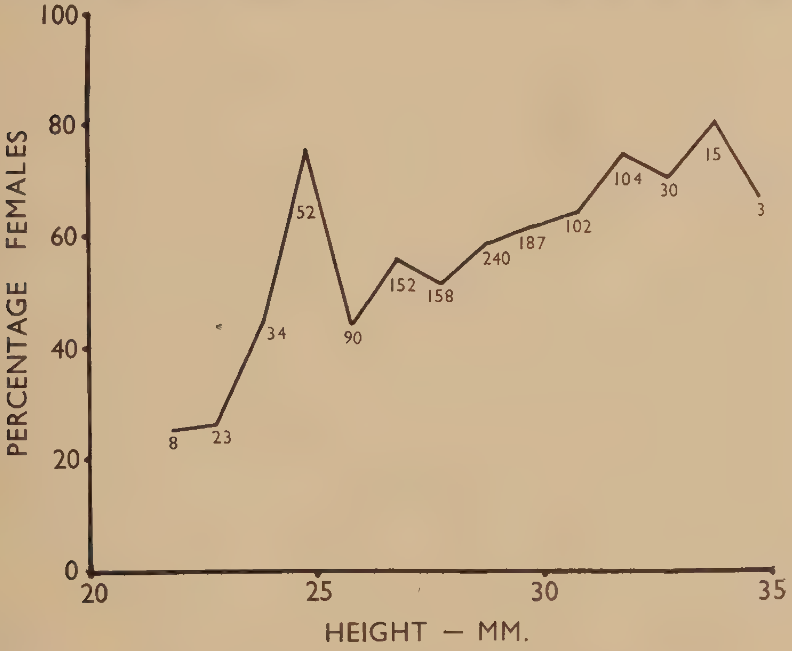


Fig. 6. Variation in the percentage of females in relation to size, in a sample of *Purpura* from Drake's Island. Figures indicate numbers examined.

Although the experiments with marked shells failed to show any difference in the rates of growth of males and females, a test was made to see whether the two sexes matured at the same size. The material was collected from Drake's Island in July 1935, and 1195 individuals of the mature, thick type, were examined. Sex was determined by the presence or absence of a penis. The size distribution for each sex was then determined in millimetre groups. Females were more abundant in the ratio of 700 to 498, and, as shown in Fig. 6, the proportion of females increases in the larger sizes. This increase could not be accounted for by protandrous hermaphroditism, since growth ceases at maturity in both sexes, and must be due to some inherent difference in growth rate or age at maturity of the two sexes. Actually this increase chiefly affects those individuals whose size departs far from the mean, the mean sizes of the two sexes being 28·77 ± 0·088 mm. for the females, and 28·18 ± 0·105 mm. for the males, the difference, 0·59 ± 0·137 mm., being small but significant. Pelseneer also (1935, pp. 414–15) notes the high proportion of females in this species, and that the proportion increases with age.

In conclusion I wish to express my great indebtedness to all those who have assisted in the collection of this material, and in particular the staff of the Plymouth Laboratory, Dr A. Gibson, Mr J. R. Bruce, and Messrs W. Searle and C. Haughton.

REFERENCES

Colton, H. S., 1916. On some varieties of *Thais lapillus* in the Mount Desert region, a study of individual ecology. *Proc. Acad. Nat. Sci. Philadelphia*, Vol. LXVIII, pp. 440–54.

Moore, H. B., 1936. The biology of *Purpura lapillus*. I. Shell variation in relation to environment. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 61–89.

— 1937. The biology of *Littorina littorea*. Part I. Growth of the shell and tissues, spawning, length of life and mortality. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 721–42.

— 1938. The biology of *Purpura lapillus*. Part III. Life history and relation to environmental factors. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 67–74.

Pelseneer, P., 1935. *Essai d'éthologie zoologique d'après l'étude des mollusques*, 662 pp. Brussels.

THE BIOLOGY OF *PURPURA LAPILLUS*. PART III. LIFE HISTORY AND RELATION TO ENVIRONMENTAL FACTORS

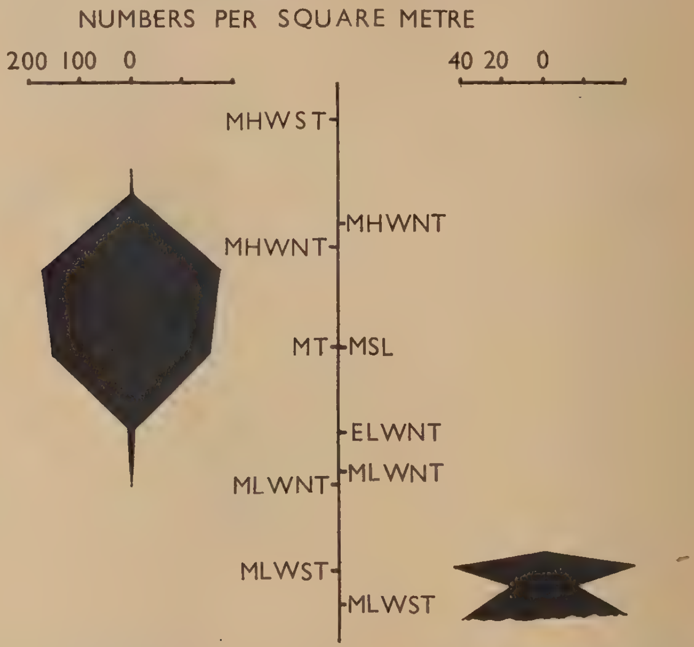
By Hilary B. Moore, Ph.D.

Bermuda Biological Station, Bermuda

(Text-fig. 1 and Plate I)

Life History

The eggs of *Purpura* are laid in vase-shaped capsules, attached in clusters to the rocks. Spawning takes place throughout the year, but chiefly in the winter and spring (Pelseneer, 1935; Moore, 1938; Colton, 1916). It is said to take more than an hour to produce one capsule, and 24 hr to produce ten (Pelseneer, 1935, p. 508), and the number of capsules laid at one time is said to average fifteen, and to range from six to thirty-one (Pelseneer, 1935, p. 490). Cooke (1895, p. 124) states that a single *Purpura* produces as many as 245 capsules. The capsules contain a large number of yolky eggs, the estimates of the numbers of these per capsule varying from three hundred to a thousand (Colton, 1916; Pelseneer, 1935, p. 527). Most of these ova are unfertilized and serve as food for the few embryos which develop: five to forty according to Pelseneer (1935, p. 481), ten to twelve according to Colton (1916). The time of development is about 4 months (Pelseneer 1935, p. 527). The capsules are laid in crevices in the rocks, or sometimes under stones, but at the same tidal level as that inhabited by the adults. The young, when hatched, are generally supposed to retreat into cracks in the rocks, presumably at the same level, and Colton states that they feed there on small *Mytilus*. I myself have examined many such crevices close to hatching groups of *Purpura* eggs, but have rarely found young shells less than 5 mm. high in them. On the other hand I have frequently found numbers of young *Purpura* down to 2 mm. in height living among the tubicolous polychaete *Spirorbis borealis* on the underside of stones at a much lower tidal level than that inhabited by the adults, and have come to the conclusion that this is their normal habitat for the first few months. And, since the distance would be great for such small shells to walk, it seems probable that they are washed down there by wave action, from the capsules from which they have hatched. In experiments in a tidal tank (Moore, 1938), it was found that the newly hatched *Purpura* would not eat even very small barnacles, but lived well on a diet of *Spirorbis*. It was noticed further, that at a height of about 8–10 mm., they showed a tendency to climb out of the tank as if conditions there did not suit them, and that this tendency was stopped if they were provided with some stones covered with barnacles. It is probable therefore that at about this size they normally change their diet and begin to move up the shore on to the barnacle-covered rocks, and it is at about this size that they are first found there in any numbers. Probably even then they at first spend a good deal more of their time sheltering in crevices than do the larger individuals, a possibility which has already been suggested on the ground of shell coloration (Moore, 1936, p. 82). The difference in tidal level of the young and adult habitats is clearly brought out in Text-fig. 1.



Text-fig. 1. Vertical distribution of adult *Purpura* (> 10 mm.) at Òb Allt an Daraich, on barnacle-covered rocks (left), and of young (< 10 mm.) under *Spirorbis*-covered stones at Wembury (right). Note that, owing to tidal differences in the two localities, the relative tidal levels do not exactly coincide.

The diet which the adult *Purpura* seems to prefer is barnacles, either *Balanus balanoides* or *Chthamalus stellatus*. They do not bore the shells of the barnacles, but force the valves apart and then eat out the soft parts. Dubois (1909), in discussing the extremely toxic nature of purpurin, suggests that the animal may use it to kill and relax its prey so that it can force the valves apart and attack the exposed body. It is quite possible that this may happen with barnacles, although nothing can be seen of the process, since the greater part of the barnacle is covered by the foot of the *Purpura* attacking it. Various gastropods are attacked by *Purpura* including *Patella vulgata*, *Gibbula cinerarea* and *G. umbilicalis*, *Littorina littorea*, *L. obtusata* and even sometimes *Purpura* itself, although in the last-named I have never seen a shell which was bored right through. The hole has been shown to be bored entirely by the radula, unaided by any acid secretion (Pelseneer, 1935). The mollusc which is most subject to attack, and in some places comprises the entire diet of the *Purpura*, is the mussel *Mytilus edulis*. Fischer-Piette (1935) has given an extremely interesting account of the changes which took place on a piece of shore which was at first inhabited mainly by barnacles and by *Purpura* which fed on them. Over this shore there was an invasion of *Mytilus*, and gradually the *Purpura* ate all the available barnacles and found themselves forced to eat the mussels. Apparently they did this at first only when forced to, taking by preference their accustomed diet of barnacles. Their efforts to penetrate the mussels, which had never before been included in their diet, were at first clumsy. Some wasted time by boring holes in empty shells, and some even settled inside empty shells and bored a hole outwards. After a time these mistakes became less frequent and finally ceased, and later still the *Purpura* learned to force apart the valves of the smaller shells without having to bore them at all. Finally the *Purpura* killed so many mussels that the barnacles, which had been displaced from the rocks, were able to recolonize them, and eventually the *Purpura* returned to their original barnacle diet. This slowness of the *Purpura* in learning to utilize mussels when these first colonize a normally barnacle-covered rock has been noted elsewhere also, and may account for the fact that in some places where the barnacle-covered rocks have small patches of mussels growing on them, the latter are left completely untouched by the *Purpura* which are feeding all round them on the barnacles, while in other apparently similar situations the bulk of the *Purpura* are feeding on the mussels, and a few only are on the barnacles. Fischer-Piette noted that when the barnacles recolonized the rocks the *Purpura* did not attack them until they were some six months old and had attained a fair size.

The mortality which they cause is very great: as described by Fischer-Piette it was sufficient to change the whole balance of life on a piece of shore. An estimate for the mortality rate of *Balanus balanoides* made at Port Erin (Moore, 1934, p. 860) was 35 and 21 % per annum at the two lower stations worked, this being probably almost entirely due to *Purpura* although these particular rocks were frequently cleared of all *Purpura*, as they were wanted for experiments on the growth of the barnacles. The rate would no doubt be much greater on rocks habitually crowded with *Purpura* like those shown in Plate I, fig. 1.

The *Purpura* do not feed continuously, and are frequently found clustered in large numbers in crevices, either for shelter or for the purpose of breeding. According to Fischer-Piette (1935) they are driven to shelter by extreme cold or by the risk of drying up, and they then pass into a state of aestivation. Probably this also is liable to happen after a large meal, and he notes that those which are living among clusters of mussels are frequently trapped at such times by the mussels' byssus threads, which become attached to their shells and anchor them so firmly that they are unable to escape and so die.

Relation to Environmental Factors

There are very few observations available on the tolerance of this species to variation in the environment, although certain notes on limiting values have been made. With regard to tidal level, Colman (1933) says that *Purpura* occurs at Wembury from one foot above mean sea level to half way between mean and equinoctial low water of spring tides, that is from 55 to 10 % emersion. Fischer-Piette (1936) gives its upper limit as high water of neap tides. It certainly does not extend above the upper limit of barnacles, and this is usually about high water of neap tides, unless elevated by splash. Usually, however, *Purpura* becomes less abundant some way below the top of the barnacle zone. Its lower limit is less well defined and varies greatly from one place to another. It can certainly live in the sublittoral zone in some places, and even down to a depth of 10 fathoms (Moore, 1936, p. 84), but this is unusual; extreme low water of spring tides is probably its normal lower limit, and its occurrence even as low as this will depend on the presence of barnacles or other suitable food at that level. In sheltered waters barnacles may not go below half-tide level, and unless there are *Mytilus* present the *Purpura* also will stop at that level. The above statement applies only to the larger sizes, above about 10 mm. in height. The young, as has already been shown, live in the *Spirorbis* zone which frequently takes the place of the *Balanus* zone towards low water, and all those places where we have found very small *Purpura* in abundance have been about low water of spring tides. It is usually difficult to find sufficiently large unbroken surfaces on which to make comparative counts of the density of population of the larger *Purpura* at the different levels, but Text-fig. 1 shows the result of such a count made at Òb Allt an Daraich, in Skye, one of the levels being also shown in Pl. I, fig. 1. The distribution of small *Purpura*, at a stage when they are still feeding on *Spirorbis*, made in a stony gully at Wembury, Devon, is also shown in Text-fig. 1, for comparison with the zonation of the adults.

Gowanloch (1927) gives the upper lethal temperature for *Purpura* as 35–35·5° C.; and the proximity of its northern limit of distribution to the 0° C. winter isotherm (Moore, 1936) suggests the presence of ice as the limiting factor there. Colton (1916) also comments on its absence from places where ice accumulates, whilst Gislén (1930) states that in the Gullmar Fjord it descends below low water for the winter, presumably to avoid the ice. Caullery (1929) has noted it as one of the species which suffered from the coincidence of a very cold spell during the winter on the Boulogne coast with the occurrence of low water of spring tides, and Orton & Lewis (1931) record the effect of the unusually cold weather in January–February 1929 in greatly reducing the proportion of *Purpura* to *Urosalpinx* on the oyster beds of the Blackwater estuary. On the latter occasion, however, it is not possible to say whether the result was directly due to the low temperature or perhaps to a reduction of tolerance to low salinity produced by the lowering of the temperature, comparable with that recorded by Broekhuysen (1936) for *Carcinus maenas*.

Its tolerance to low salinity is probably low, despite Pelseneer's statement (1935, p. 323) that it can survive 9·5 days in fresh water. Fischer (1928) records it in the estuary of La Rance between the salinities of 35·0 and 22·8 $^{\circ}/_{\circ\circ}$; Alexander, Southgate & Bassindale (1935) also state that it is confined to the extreme mouth of the Tees estuary (which, however, is strongly polluted), and it certainly does not penetrate beyond the extreme mouths of the Tamar and Yealm estuaries at Plymouth. Ökland also (1933) has shown that round the island of Tromö, *Purpura* does not occur where the summer salinities fall below 20–25 $^{\circ}/_{\circ\circ}$, even where *Mytilus* and *Balanus balanoides* offer abundant food for it. Fischer (1928) states that the eggs are tolerant of the same salinity range as the adults, but he found (1931), during a winter drop in salinity in La Rance estuary, that the eggs were killed although the adults survived.

With regard to limiting values of other factors there are practically no data available. Fischer (1927) gives its upper limit of *p*H in pools as 9·3, and later (1931) gives its *p*H range in pools as 9·3 to 7·45. He also gives its oxygen range in pools as 26 to 5·8 mg. per l. These figures however mean little without a knowledge of how long such conditions can be endured. *Purpura* occurs occasionally, though not commonly, in muddy surroundings, where it has the appearance of having been introduced accidentally and not having bred there. At Blue Anchor Bay, near Minehead, just beyond the extreme eastern limit of penetration of *Chthamalus stellatus* up the south side of the Bristol Channel, no *Purpura* were found, although *Balanus balanoides* was present in small numbers. The limiting factor here was probably the muddiness of the shore.

ENEMIES

There are no data available at present as to the mortality rate or normal duration of life of *Purpura*. Several marked individuals lived on the shore at Port Erin for $2\frac{1}{4}$ years, and were probably $1\frac{1}{2}$–$2\frac{1}{2}$ years old when first marked, but they can probably live much longer than this. If the rings found on the shells of *Purpura* by Colton were really annual, then the oldest specimens recorded by him were 7 years old, but these must have been much slower in maturing than is normal in England, since at maturity they would stop growing and form no more annual rings, that is if cessation of growth occurs at all in his communities.

Various animals are recorded as occasionally eating *Purpura*, although most of them probably do not take sufficient numbers to have any appreciable effect on the community as a whole. Colton (1916) suggests that they may be taken by *Gadus virens* at Mount Desert Island, and probably wrasse sometimes take them in English waters. Bauer (1913) has found that shells of *Nassa* inhabited by hermit crabs frequently show a fracture of the last whorl which suggests that they have been broken open by the crab and the animal eaten out of them. He further suggests that the thickening of the lip found in some species of *Nassa* is a protection against the attacks of hermit crabs. Since empty shells of *Purpura* also are frequently found inhabited by hermit crabs the same suggestions would presumably apply to them, but my own impression is that they occupy only shells which are already empty, and that the fractured shells found are the work of birds.

Probably the most serious enemies of *Purpura* are birds, and these in certain localities only. Dewar (1910) has given a detailed account of how *Purpura* shells are broken open by oyster-catchers (*Haematopus ostralegus*). The *Purpura* are removed from the rock and carried either to a crevice or to a patch of firm sand where they can be held steady. They are then turned with the opening up, the lower part of the bill inserted between the operculum and the outer lip, and a piece of this lip broken away either by pressure or by hammering. The shell is then turned slightly and a second chip broken away in a similar manner, by which time the animal is sufficiently exposed for the soft parts to be picked out of the shell. A good many shells resist the attacks of the birds. In a later paper (1913) Dewar records that out of 294 *Purpura* attacked by oyster-catchers, 1 % had only one chip removed, 21 % were completely opened (two chips), while 78 % remained undamaged. He states also (1910) that *Purpura* is an uneconomical food for the oyster-catcher as compared with mussels. In 20 min. a single bird attacked seven shells and opened three of them, whereas many more mussels could have been opened in the time, and he says further that they only eat the *Purpura* sporadically, having a habit of feeding on them for a few days and then leaving them again completely. Colton (1916) says that herring gulls (*Larus argentatus*) eat them, swallowing the smaller shells whole, but carrying the larger shells into the air and dropping them until they break. He says too that on certain islands where the gulls are particularly numerous, the *Purpura* are practically exterminated. In the British Isles gulls certainly take *Purpura* at times as shown in Plate I, fig. 2, which is a photograph of part of the contents of a herring gull's nest containing numerous *Purpura* shells; but an examination of numbers of heaps of shells regurgitated by herring gulls on different parts of the coast shows that, while they may at times be feeding almost entirely on molluscs, *Purpura* forms only a very small proportion of their food.

The *Nassa* shells with a chip out of the lip, attributed by Bauer to the action of hermit crabs, seem to be very similar to those chipped open by oyster-catchers, and similarly chipped shells of *Purpura* have been found by us on grounds where oyster-catchers were common. Quite frequently the animal escapes, although with a damaged shell, and the proportion of shells showing a repaired fracture is high in some populations. Probably a similar cause accounts for the populations in which many of the animals have a damaged operculum or none at all. Cooke (1917) records one such population in which, out of 121 animals examined, fifty-six had damaged opercula, and eleven had none. Other birds also may attack *Purpura* on occasions, and there is even a record by Venables (1936) of a song-thrush which was seen hammering a *Purpura* on a stone during a spell of very cold weather, with a heap of dead *Purpura* shells alongside.

The shells may be attacked by boring algae such as *Gomontia* and *Plectonema* (Moore, 1936), and even very seriously pitted by their action, and the shell may also be damaged by the boring sponge *Cliona cellata* and the polychaete *Polydora*; but it is unlikely that any of these ever kill the animal, since it is able to repair a damaged shell. Various trematode parasites infect the soft parts and may destroy the reproductive organs, but probably these also rarely kill the animal.

REFERENCES

Alexander, W. B., Southgate, B. A. & Bassindale, R., 1935. Survey of the river Tees. Part II. The estuary—chemical and biological. *Dept. Sci. Indust. Res., Water Pollution Res.*, Tech. Paper No. 5, pp. 1–171.

Bauer, Victor, 1913. Notizen aus einem biologischen Laboratorium am Mittelmeer. *Internat. Rev. Hydrobiol. Hydrogr.*, Bd. vi, Heft 1–3.

Broekhuysen, G. J., 1936. On the development, growth and distribution of *Carcinides maenas* (L.). *Arch. Néerland. Zool.*, Tome ii, pp. 257–399.

Caullery, M. M., 1929. Effets des grands froids sur les organismes de la zône intercotidale dans le Boulonnais. *Bull. Soc. Zool. France*, T. liv, pp. 267–9.

Colman, J., 1933. The nature of the intertidal zonation of plants and animals. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 435–76.

Colton, H. S., 1916. On some varieties of *Thais lapillus* in the Mount Desert region, a study of individual ecology. *Proc. Acad. Nat. Sci. Philadelphia*, Vol. lxviii, pp. 440–54.

Cooke, A. H., 1895. Molluscs, pp. 1–459. In *The Cambridge Natural History*. London: MacMillan & Co.

— 1917. A colony of *Nucella lapillus* (Linn.) with the operculum malformed or absent. *Proc. Malac. Soc.*, Vol. xii, pp. 231–2.

Dewar, J. M., 1910. A preliminary note on the manner in which the oyster-catcher (*Haematopus ostralegus*) attacks the purple-shell (*Purpura lapillus*). *Zoologist*, 4th Ser., Vol. xiv, pp. 109–12.

— 1913. Further observations on the feeding habits of the oyster-catcher (*Haematopus ostralegus*). *Zoologist*, Vol. xvii, pp. 41–56.

Dubois, R., 1909. Recherches sur la Pourpre et sur quelques autres pigments animaux. *Arch. Zool. Exp. Gén.*, 5e Sér., T. ii, pp. 471–590.

Fischer, E., 1927. Sur la tolérance de quelques espèces d'animaux du littoral, vis-à-vis les variations de *p*H. *Bull. Inst. Océanogr., Monaco*, No. 505, pp. 1–4.

— 1928. Recherches de bionomie et d'océanographie littorales sur La Rance et le littoral de la Manche. *Ann. Inst. Océanogr.*, T. v, f. 3, pp. 201–429.

Fischer-Piette, E., 1931. Sur la pénétration des diverses espèces marines sessiles dans les estuaires et sa limitation par l'eau douce. *Ann. Inst. Océanogr.*, T. v, f. 8, pp. 215–43.

— 1935. Histoire d'une mouliere. *Bull. Biol. Fr. Belg.*, T. lxix, pp. 152–77.

— 1936. Études sur la biogéographie intercotidale des deux rives de la Manche. *Journ. Linn. Soc.* London, Zool., Vol. xl, pp. 181–272.

Gislén, T., 1930. Epibioses of the Gullmar Fjord. I and II. *Kristinebergs Zool. Stat.* 1877–1927, Uppsala, pp. 1–123 and 1–380.

Gowanloch, J. N., 1927. Contributions to the study of marine gastropods. II. The intertidal life of *Buccinum undatum*, a study in non-adaptation. *Contr. Canad. Biol. Fish.*, N.S., Vol. iii, pp. 167–77.

Moore, H. B., 1934. The biology of *Balanus balanoides*. I. Growth rate and its relation to size, season and tidal level. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 851–68.

Moore, H. B., 1936. The biology of *Purpura lapillus*. I. Shell variation in relation to environment. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 61–89.

— 1938. The biology of *Purpura lapillus*. Part II. Growth. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 57–66.

Ökland, F., 1933. Litoralstudien an der Skagerrakküste Norwegens: die Verbreitung von *Purpura lapillus*, *Patella vulgata* und den *Littorina*-Arten in Tromö. *Zoogeographica*, Bd. 1, Heft 4, pp. 579–601.

Orton, J. H. & Lewis, H. M., 1931. On the effects of the severe winter of 1928–9 on the oyster drills (with a record of five years' observations on sea temperature on the oyster beds) of the Blackwater estuary. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 301–13.

Pelseneer, P., 1912. Recherches sur l'embryologie des gastropodes. *Acad. Roy. Belg.*, *Cl. Sci.*, 2me Sér., T. iii, pp. 1–167.

— 1935. *Essai d'éthologie zoologique d'après l'étude des mollusques*, pp. 1–662.

Venables, L. S. V., 1936. Thrush eating *Purpura*. *British Birds*, Vol. xxix, No. 9, p. 288.

EXPLANATION OF PLATE I

Fig. 1. *Purpura* feeding on *Balanus balanoides* at Òb Allt an Daraich, Skye. 12. vi. 36.

Fig. 2. Part of the contents of a herring gull's nest, Geodha Chobhair, Sutherland, 24. vi. 36, showing fragments of *Purpura lapillus*, *Patella vulgata*, *Balanus balanoides*, *Cancer pagurus*, *Portunus puber* and egg shells. ×0·81.

PLATE I.

1

2

John Bale Sons & Curnow, Ltd London

AN INTERNAL FACTOR CONTROLLING POSTERIOR REGENERATION IN SYLLID POLYCHAETES

By Yô K. Okada

Kyoto Imperial University, Japan

(Text-figs. 1–3)

In a former paper (1929) it was stated that "regeneration takes place easily at the posterior end of divided syllids, but on cutting the most anterior part, the chitinous tube and massive proventriculus of the pharynx hinder the process of closing the wound and subsequent regeneration fails in most cases". The minimum length of so-called head pieces, in which regeneration of the tail can be effected, always comprises at least one or two more segments than those constituting the pharyngeal region. This length is internally occupied by a large chamber containing a series of highly specialized organs of ectodermal origin, extending as far as the first appearance of the moniliform intestine in a segmental cavity, which is separated from the previous one by a complete septum.

The peripharyngeal chamber is of different lengths in different species. The shortest length of the head pieces, which give caudal regeneration, also differs according to the species. The nature of this correlation between the anterior differentiation of segments and their physiological property of regeneration at the posterior end, is not yet elucidated. If, however, the cause of failure to regenerate at the posterior end in a head portion cut at the extreme anterior part of the body be assigned to the absence of certain internal structures in such an anterior portion, the formative factor of the posterior regeneration should then be correlated with the existence of such structures in the pieces and not with the physiological property of the segments involved.

Experiments with reference to this question were performed, during the summer of 1927 when I was working at the Plymouth Laboratory, on *Autolytus edwarsi*, which is very abundant in this district in close association with the hydroid *Obelia geniculata*. The anterior chamber of the species is composed of cavities corresponding to 9 or 10 anterior segments and the tail regenerates only beyond the 11th setigerous segment.

In the first series of experiments the animals were cut across at different levels of the pharyngeal part within the bounds of the region presumptively non-regenerative at the posterior end, after the intestine was forced into the anterior chamber. This was done by pressing the proventriculus forward forcibly with the back of a knife. This procedure made it possible, provided exceedingly anterior levels were not operated on, to retain a bit of the intestine in the isolated head pieces. The latter closed the wound more easily and the specimen lived longer than in the former experiments when the cut was made simply at the corresponding levels of the body. Moreover, some pieces were detected, when observed about 2 weeks later, regenerating more or less segments at the posterior end (see Fig. 1). The operation was repeated several times until a sufficient number of specimens was obtained to give conclusive results. From the results the following two facts emerged:

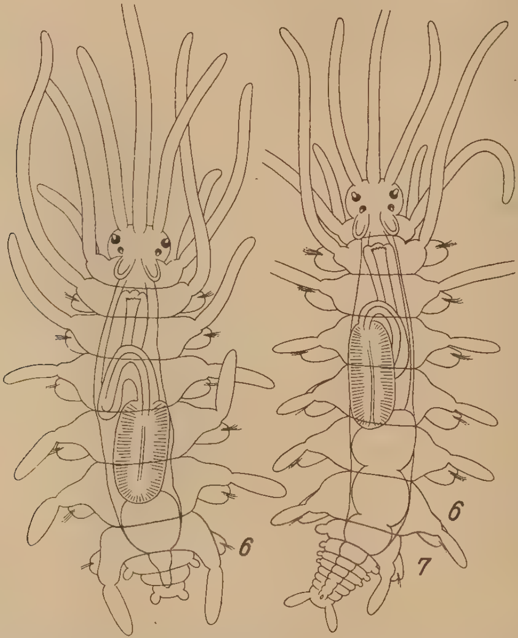


Fig. 1. Tail regeneration in short head pieces of *Autolytus edwarsi* in the presence of the intestine.

(1) Regeneration can take place posteriorly from any level after the 6th setigerous segment backwards, and this level at which posterior regeneration ceases is quite definite. For example, the anterior pieces isolated between the 5th and the 6th segments do not produce a tail, but if a small fragment of the 6th segment remains attached to the posterior end of the 5th segment, regeneration occurs at this end (see Fig. 2).

(2) Where regeneration occurs, the tail does not develop beyond the state of the pygidium, unless the intestine elongates and is in close contact with the body wall at the posterior end. It is only when the last mentioned condition

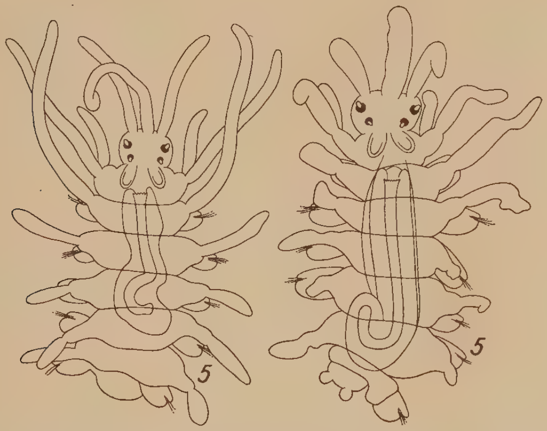


Fig. 2: Experimental demonstration of the anterior limit of tail regeneration of *Autolytus edwarsi.*

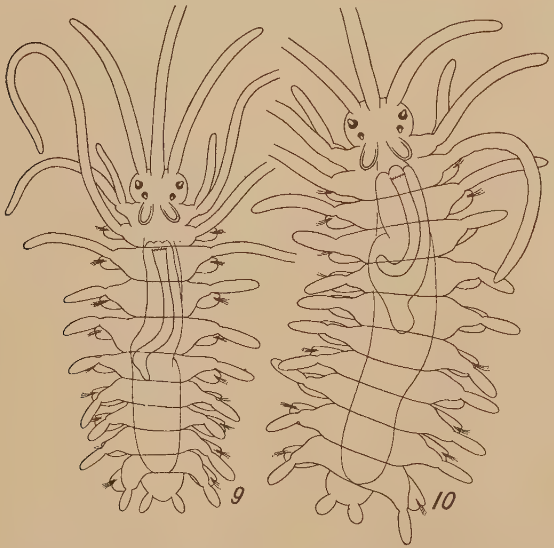


Fig. 3. Incomplete tail regeneration in long head pieces of *Autolytus edwarsi* in the absence of the intestine.

is fulfilled that the development proceeds further and a long tail is produced.

That the intestine plays an important role in the caudal regeneration of the syllid is obvious. But it remains for us to show what the role is.

Thereupon the intestine was removed from fairly long anterior pieces in which caudal regeneration is normally possible. This operation was done by pressing down the proventriculus with the back of a knife and drawing it out through the wound at the posterior end by a fine hooked needle. A cut was then made in front of the pushed-down proventriculus, and the more posterior part of the alimentary canal was removed including the intestine. The animals operated on lived well as in the preceding experiment. They closed the wound and most of them regenerated a tail, which, however, did no more than develop a caudal extremity (see Fig. 3). A pair of anal cirri was quite distinct but there appeared no other segments beside the pygidium.

From the second experiment it now becomes clear that the intestine is necessary for elongation and segmentation of the new tail. The intestine itself does not seem to modify the nature of regeneration. Nevertheless, none of these regenerates without the intestine produced a heteromorphic head.

REFERENCE

OKADA, YÔ K., 1929. Regeneration and fragmentation in the syllidian polychaetes (Studies on the Syllidae II). *Arch. Entwicklungs. Org.*, Bd. 115, pp. 542–600.

ON THE OCCURRENCE OF *JAXEA NOCTURNA* (CHIEREGHIN) NARDO OFF RAME HEAD, DEVON

By Ruth Rawlinson, M.Sc.
The University, Liverpool

(Plate II)

A single specimen of the rare thalassinid *Jaxea nocturna* was recently dredged from mud off Rame Head, Devon, by S.S. *Salpa* on September 3 1937 during the September Vacation Course at the Plymouth Laboratory. Prior to this there are only four records of the adults of this species in waters round the British Isles although they are abundant in the Adriatic Sea. Selbie (1915) summarizes the British records as far as 1914. The first individuals were taken as fragments from the stomachs of gurnards and *Pleuronectes cynoglossus* captured in the Firth of Clyde near Ailsa Craig (Scott, 1899); the next was from the Irish Sea, in mud, off Clogher Head, Co. Louth, at a depth of 32½ fathoms and in 1908 one was taken in Loch Fyne in 34 fathoms. The next record is a single specimen taken by Mr G. A. Stephen on March 26 1936 from the mud two miles south of Rame Head, and at a depth of 24 fathoms. Since September 3 1937 four more have been captured in the same locality, one on September 28 1937 and three on October 6 1937, using a new type of dredge.

The trachelifer larvae of *Jaxea nocturna* are quite widely distributed in British waters. They have been recorded from the Irish Sea and the west coast of Ireland (Selbie, 1915); the Clyde Estuary, and Tobermory, Mull (Scott, 1899); Barrow Channel, off Piel and Tremadoc Bay, Caernarvon (Scott, 1905); the English Channel between Looe and Eddystone (Bouvier, 1914); Plymouth Sound (Lebour, 1916) and Salcombe (Norman & Scott, 1906).

All the 1937 Plymouth adults, as far as one can judge without dissection, agree closely with the description of *J. nocturna* by Selbie (1915). One male and one female have been dissected for a careful examination of the body segments, appendages and gills. They show only minor points of difference from Selbie's account. Three teeth were present in the male on the anterior edge of the first pleura, as in Selbie's account, but they were absent from one side of the female and there was only one tooth on the other. The fifth pleura of two females were rather more rounded at the apex than figured by Selbie, but in the rest they were as figured by him. The second maxillipede is somewhat different. The epipodite has a distinct twist towards the proximal end and the merus bears long setae on its outer margin (Plate II, fig. 3).

Three of the Plymouth individuals were females and the other two males. The only obvious difference between the sexes is the absence of the first pair of pleopods from the male. Two of the specimens were approximately 36 mm. from the tip of the rostrum to the tip of the telson, and the others about 34 mm. The chelae, measured from the proximal end of the merus to the tip of the dactylopodite are about three-quarters the length of the body. Selbie's drawing gives the impression of a much longer chela than is present in the Plymouth specimens, but there is not really very much difference between them (see Plate II, fig. 1).

The specimen captured on September 3 1937 was kept alive in the laboratory until December 29 1937 at an average temperature of 57·1° F. in October, 52·7° F. in November, and 49·5° F. in December. During this time intermittent attempts were made to study its mode of feeding. It was kept in a square glass dish containing a layer of sand about an inch deep, and provided at various times with shreds of fish, *Mytilus*, living *Polystomella* and plankton. None of these were apparently eaten and, with the exception of the *Mytilus*, which was toyed with by the second peraeopods, all were ignored. The second pair of peraeopods are usually extended forwards beneath the head (Plate II, fig. 2), so that their tips are visible beneath the antennae when viewed from the dorsal surface. Their dactylopodites are flattened and may be folded back against the next segment. By their movements, fine particles are disturbed from the substratum and whisked towards the mouth. At intervals the third maxillipedes sweep downwards in a plane at right angles to the ground and may possibly capture particles disturbed by the second pair of walking legs. The chelae are held outstretched in front of the head and do not perform any definite movements apart from a regular swaying from side to side as the animal walks. The inner margin of their dactylopodites bears a fringe of long setae which are frequently thickly coated with fine particles. The animal did not make any attempt to burrow in the sand and unfortunately died before there was an opportunity of providing it with finer and deeper mud, as had been intended. The few observations which have been made on the movements of its appendages show resemblances to the burrowing and feeding movements described in *Callianassa californiensis* and *Upogebia pugettensis* by MacGinitie (1930, 1934). *Callianassa californiensis* uses its second and third pairs of legs as shovels, and also to sift the sand from the sides of the burrow for the detritus which accumulates on their setae; the detritus is scraped off by the third maxillipedes and then passed to the mouth. *Upogebia pugettensis* lives in mud burrows, feeding on suspended material. It holds its first and second walking legs so as to form a basket through which water is drawn from the entrance of the burrow by the movements of the swimmerets. The sieved particles are swept out of the basket at intervals by the outward and downward movements of the third maxillipedes and pass via the second maxillipedes to the mouth. If *Jaxea nocturna* lives in mud burrows, possibly between rocks, in places inaccessible to the usual dredging methods, the movements of the second pair of walking legs and the third maxillipedes suggest that its feeding mechanism is similar to that of the species described by MacGinitie. Whether *Jaxea* uses the fringed chelae to construct a basket like *Upogebia pugettensis*, scrapes sand like *Callianassa californiensis* Dana, or has some different, but probably very similar feeding method, is not known. These members of the Callianassidae, like some other detritus and suspension feeders of the tribe Anomura, use their third maxillipedes to sweep off food particles gathered by the anterior walking legs towards the mouth. One or more of the first three pairs of peraeopods is used by the three species described above. Among the Paguridae, *Eupagurus bernhardus* employs only the smaller claw of the first pair of peraeopods to gather food, which is passed on to the third maxillipedes (Orton, 1927), whereas other anomurans, for example *Galathea dispersa* and *Porcellana longicornis*, use their third maxillipedes to gather food particles from the substratum or from the water (Nicol, 1932).

My thanks are due to Dr Kemp for the loan of the four additional Plymouth specimens of *Jaxea nocturna*, and his permission to dissect one of them, and to Mr D. P. Wilson for the photograph published as fig. 1 in Plate II.

REFERENCES

Bouvier, E. L., 1914. Observations nouvelles sur les trachelifer, larves lucifériformes de *Jaxea nocturna*. *Journ. Mar. Biol. Assoc.*, Vol. x, pp. 194–206.

Lebour, M. V., 1916. The microplankton of Plymouth Sound from the region beyond the breakwater. *Journ. Mar. Biol. Assoc.*, Vol. xi, pp. 133–182.

MacGinitie, G. E., 1930. The natural history of the mud shrimp *Upogebia pugettensis* (Dana). *Ann. Mag. Nat. Hist.*, Ser. 10, Vol. vi, pp. 36–44.

— 1934. The natural history of *Callianassa californiensis* Dana. *Amer. Mid. Nat.*, Vol. xv, pp. 166–77.

Nicol, E. A. T., 1932. The feeding habits of the Galatheidea. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 87–106.

Norman, A. M. & Scott, T., 1906. *The Crustacea of Devon and Cornwall*, pp. 12–13.

Orton, J. H., 1927. On the mode of feeding of the hermit-crab, *Eupagurus bernhardus*, and some other decapoda. *Journ. Mar. Biol. Assoc.*, Vol. xiv, pp. 909–21.

Selbie, C. M., 1915. The decapod Reptantia of the coasts of Ireland. *Dept. Agric. Tech. Instr. Ireland. Fisheries Branch. Sci. Invest.* (1914), 1–116 pp.

Scott, A., 1905. On tow-nettings collected in the Irish Sea. *Trans. L'pool Biol. Soc.*, Vol. xix, pp. 196–215.

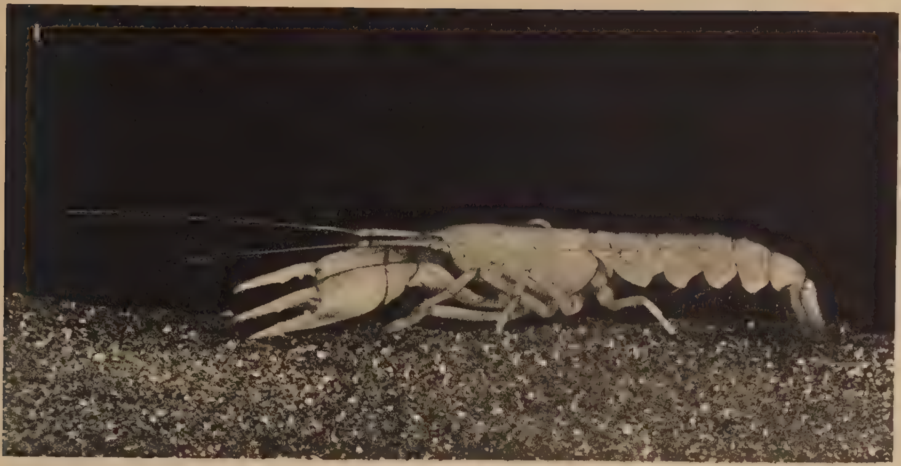
Scott, T., 1899. Notes on recent gatherings of micro-crustacea from the Clyde and Moray Firth. 17*th Ann. Rep. Fish. Board Scotland*, Pt. iii, pp. 248–73.

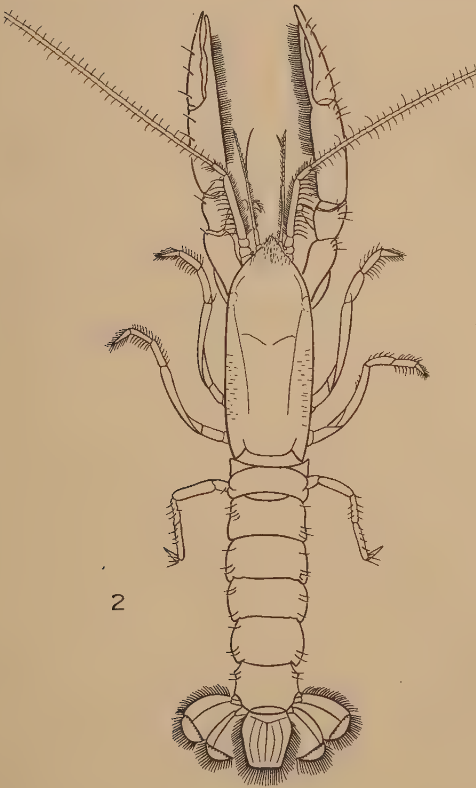
EXPLANATION OF PLATE II

Fig. 1. Side view of *Jaxea nocturna* ♂ (3. ix. 37). × 1·7. (Photograph by Mr D. P. Wilson.)

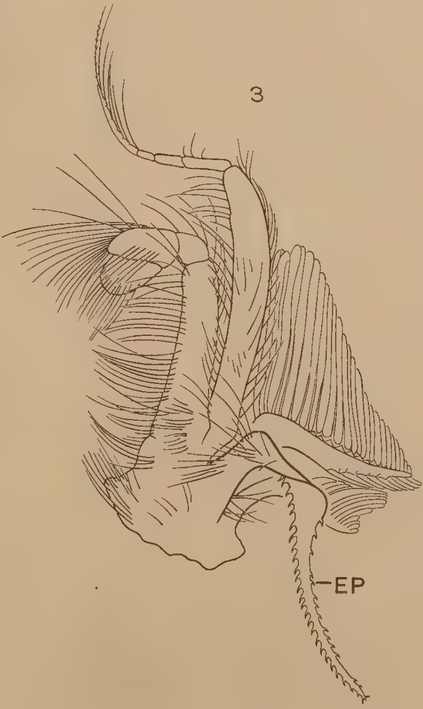
Fig. 2. *Jaxea nocturna* (♂), drawn from the living animal captured 3. ix. 37, from Rame mud, Plymouth. × 2·2.

Fig. 3. The second maxillipede of *Jaxea nocturna* showing the twisted epipodite. × 17.





2



3

John Bale, Sons & Curnow, Ltd London.

THE INTERTIDAL FAUNA OF THE MERSEY ESTUARY

By R. Bassindale, M.Sc.

Assistant Lecturer in Zoology, Manchester University

(Plate III)

INTRODUCTION

During a general survey of the tidal banks of the Mersey Estuary observations on the nature of the banks and on the density of the burrowing animals inhabiting them were made and were supplemented by the identification of the more common macroscopic types found.

The positions of the different areas of mud and sand were determined by means of sextant angles and plotted by station pointers. These areas are shown in Plate III and reference to them in the text is made by means of the numbers shown on the Key Chart therein.

Specimens of the common macroscopic animals inhabiting the banks were preserved in formalin for subsequent identification.

The nature of the banks (whether mud or sand) and the abundance of the infauna were ascertained from inspection of the surface layers to a depth of about one foot. All the observations were made in the summer of 1933.

A detailed description of the topography and tidal conditions in the estuary, and the results of analyses of the water and of the material constituting the tidal banks and bed of the estuary, are given in *Water Pollution Research Technical Paper*, No. 7, issued by the Department of Scientific and Industrial Research (1937).

The estuary is divided into two natural divisions—the Outer Estuary or Liverpool Bay and the Upper Estuary. The Upper Estuary is that part of the estuary lying between Warrington and Rock Light. The Outer Estuary lies seaward of Rock Light and consists of a bay in which large areas of banks are exposed at low tide.

Of 37 sq. miles of tidal banks in the Outer and Upper Estuary as far as Runcorn Gap, approximately half occurs in the Outer and half in the Upper Estuary. Four-fifths (29 sq. miles) of the total area are banks of sand of which only 7½ sq. miles are inhabited (one-fifth of the total area). The remaining banks (one-fifth of the total or 7½ sq. miles) are of mud, and by far the greater area of mud occurs in the Upper Estuary, mainly along the Cheshire shore from Mount Manisty to the River Weaver. Densely inhabited mud is much commoner than sparsely inhabited or uninhabited mud, the former occupying approximately 6½ sq. miles and the two latter only 1 sq. mile.

The main bank of mud along the Cheshire shore is separated from the uninhabited sand banks, through which the channels run by a series of patches of sparsely inhabited sand or mud, and densely inhabited sand. The main mud bank is divided into two parts by the River Gowy which, entering the Upper Estuary at Stanlow, occupies a low sandy plain flanked on either side by high mud banks.

Much of the sand is formed into waves (presumably by current action), and these areas adjoin the main channels. The island banks in the Outer Estuary have a high peak directed towards the river mouth at Rock Lighthouse, and shelve away seawards.

General Description of the Infauna

The Upper (or Inner) Estuary

The Upper Estuary comprises the Narrows from Rock Light to Garston, a large basin extending from Garston to Runcorn and a smaller basin above Runcorn. Except at high spring tides Howley Weir (at Warrington) divides the tidal from the non-tidal reaches. Observations have not extended beyond Norton Marsh some 3 miles above Runcorn. As will be shown later in a comparison with other estuaries, this limits the collections to areas where freshwater animals are not normally found.

The most notable inhabitant of the banks is the brackish water polychaete *Nereis diversicolor*. This mud-living worm is found in the Upper Estuary from Norton Marsh to the Narrows wherever mud with a depth of more than a few inches occurs; it is also found in banks of mud in the Outer Estuary near the mouth of the River Alt. Large areas of the main mud bank (Areas Nos. 23 and 29, Pl. III) between Stanlow and the Weaver Sluices in the Upper Estuary are densely inhabited by this organism. At Stanlow a density of 440 per sq. m. was found from a count within a quarter metre square, and the difficulties of sieving the mud make it probable that the true figure is higher. The softer parts of the bank, in gulleys and near the Weaver Sluices, are not inhabited by *Nereis*. In these softer places a small red oligochaete, identified by Fraser (1932) at Dingle as *Clitellio arenarius*, is abundant and is the only inhabitant. In addition it usually occurs wherever *Nereis* is found. Both these forms appear to burrow more deeply into the mud when the surface has become dry and cracked during neap tides. *Clitellio* may then be found well below the surface in the form of balls containing large numbers of intertwined specimens.

At most times of the year, but particularly during the summer, the surface of the banks of mud in the Upper Estuary is covered by a green scum consisting mainly of *Euglena* sp., probably *Euglena limosa* (Fraser, 1932). The scum seems to develop most readily on the soft mud not inhabited by *Nereis*. Many species of diatoms are also found in the scum, and in places these are so abundant as to give the surface a dark green or brown colour. In certain areas, as on the mud-covered rocks at Runcorn Gap, Hale Head and Garston and occasionally on sand, there is a brown scum of diatoms without *Euglena*. Ghazzawi (1933) has identified the diatoms found on the Dingle foreshore, and in his list of some fifty species are to be found the names of fresh-water, marine and brackish-water species.

In addition to the scum of unicellular forms, the estuarine mud banks are frequently covered by a growth of a filamentous alga, *Vaucheria* sp. This alga covers the surface mud, and the tide frequently rolls up the blanket-like layer of mud and alga, and washes it away. In other parts (Area No. 33, on the foreshore near Speke) the growths appear as rounded tufts above the general level of the soft mud. *Clitellio* is the only recorded inhabitant of mud covered by *Vaucheria.*

The remaining outstanding feature of the mud banks in the Upper Estuary is the presence of the small crustacean, *Corophium volutator*, which builds small U-shaped burrows in the surface layers. It occurs over a large part of Areas Nos. 23 and 29 and in many other places. It is most abundant in the sandy mud of Area No. 27 near Stanlow and in the adjoining area of densely inhabited sand (Area No. 24) which contains a fair proportion of mud. It is in this neighbourhood that the small bivalve *Macoma balthica* is to be found, widespread and abundant in mud and muddy sand. Fraser (1932) found a maximum of 6000 *Macoma* per sq. m. at Dingle, and it is probable that the abundance in Areas Nos. 27 and 24 is similar or even greater than at Dingle. *Macoma* does not appear to tolerate soft mud nor the clayey mud of Areas Nos. 23 and 29.

The two other species of burrowing animals found commonly in the Upper Estuary are worms, and they are associated with fairly clean sand. *Arenicola marina* (the common lug-worm) is sparsely distributed in fairly large areas as far up as Area No. 22 on the bank between Dungeon Point and Hale Head. The tube-building form *Pygospio elegans* is abundant but patchy in its distribution and occurs as far up as Area No. 16.

In the Narrows at Wallasey, burrowing worms are found in greater variety than elsewhere in the Upper Estuary, seven species being recorded from Area No. 45.

The Outer Estuary (Liverpool Bay)

The Upper Estuary opens into Liverpool Bay at the corner of a right angle formed by the Cheshire and Lancashire coasts. At low tide extensive sand banks are exposed in Liverpool Bay (Pl. III). The variety of species in the Outer Estuary is much greater than in the Upper Estuary.

Of the species occurring commonly in the Upper Estuary *Nereis diversicolor* has a limited distribution in mud at the mouth of the River Alt. *Macoma balthica* and *Corophium volutator* also occur near the Alt and in mud at Hoylake. *Arenicola marina* is much more widespread and abundant and occurs over large areas. *Clitellio* was not recorded. *Pygospio elegans* occurs near the Alt but is not widespread. Of the plants recorded from the Upper Estuary *Vaucheria* and *Euglena* were not observed in Liverpool Bay. A diatom scum occurs in places but the species were not determined.

Two interesting low-lying areas of densely inhabited muddy sand occur on Taylor's Bank (Area No. 97) and on Spencer's Spit (Areas Nos. 60, 61 and 51).

At Taylor's Bank the cockle, *Cardium edule*, occurs in abundance with a few *Cardium rusticum*. The burrowing heart urchin, *Echinocardium cordatum*, with its attendant bivalve, *Montacuta ferruginosa*, and the large tube-building worm, *Lanice conchilega*, are fairly common. In addition, the molluscs *Chione striatula* and *Tornatella fasciata*, the worms *Nephthys hombergi* and *Arenicola marina* and hydroids growing on the cockles were found. Towards the edge of the cockle bed, cockles die away and *Lanice* becomes more abundant finally giving way in cleaner sand to another tube-building worm, *Owenia fusiformis*, at Areas Nos. 98, 99 and 100. The areas of sparsely inhabited sand shown in Plate III at Area No. 100 were actually more numerous than figured and consisted of gullies lying between the crests of long broad-fronted waves of sand. At Area No. 101, which consists of fine sand, the bivalve *Donax vittatus* occurs in small numbers.

The sand at Spencer's Spit has a different fauna. *Donax vittatus*, rare on Taylor's Bank, occurs at Area No. 61 in great abundance.

At Area No. 60, *Echinocardium*, with *Montacuta* and a tube-building worm, *Pectinaria koreni*, are extremely abundant. Rough estimates of the abundance of these three species gave for *Echinocardium* (mainly up to 1 in. in length) 150 per sq. m. and for *Donax* and *Pectinaria* about 300 per sq. m. Other species with *Donax* at Area No. 61 were *Echinocardium*, *Lanice*, *Arenicola* and a brittle star, *Ophiura texturata*, which was often partly buried in the sand. At Area No. 60, with *Echinocardium* and *Pectinaria*, were *Arenicola*, *Lanice* and *Donax*. In the less densely inhabited sand at Area No. 62, *Arenicola* and *Echinocardium* occurred occasionally, and, near the centre of this area, *Ophiura* occurred in enormous numbers. Numerous patches, each about 15 sq. m. in extent, were estimated to contain about 1600 individuals per sq. m. Intervening areas of similar extent contained only a few specimens. Isolated specimens of six species of burrowing worms and of the razor shell, *Ceratisolen legumen*, were also recorded from Spencer's Spit.

The adjacent area of the shore banks (Area No. 51) was similar to Area No. 60 and contained *Lanice*, *Pectinaria*, *Owenia*, *Echinocardium*, a few young *Ensis siliqua* (a razor shell), and a few *Ophiura*. A burrowing bivalve, the clam *Mya arenaria*, was common in small patches of very muddy sand.

The island banks known as the Great Burbo Bank (Areas Nos. 66–70) are composed almost entirely of coarse sand. The surface is waved and lakes occur. The North Bank is similar but does not attain the same height. It is connected to the shore banks at low water of a high spring tide. *Lanice* is sparsely distributed over low lying areas of fine rippled sand at Areas Nos. 63, 64, 66, 67 and 68. At Areas Nos. 63 and 64 *Chione* was also found, while at Area No. 65 *Chione* alone was found.

In 1933 along the Lancashire coast the shore banks were of fine sand with some mud. The sand near the Gladstone Docks contained a large amount of mud and Area No. 72 was covered by a thin layer of mud. As Formby Point was approached the sand became cleaner and only rare patches of inhabited fine sand were found at the Point. This general trend was much disturbed where the river Alt flowed across the shore. Mud inhabited by *Nereis diversicolor* occurred close to the channel of the Alt (Areas Nos. 79 and 80), and areas of muddy sand containing large numbers of *Corophium* with some *Macoma* (Areas Nos. 83 and 95) merged into the surrounding uninhabited clean sand.

A north-westerly gale covers the areas of mud and muddy sand near the Alt with a layer of clean blown sand and completely alters for a time the appearance of these banks. The channel of the Alt was artificially shortened in 1936, and the distribution of banks in this region has been completely altered.

In the fine muddy sand extending from Crosby to the Gladstone Dock, *Arenicola marina* occurred in abundance at Area No. 75 and sparsely in other areas. *Macoma* and a few species of burrowing worms were also found. A small gastropod, *Hydrobia ulvae*, occurred on the surface over most of this area of inhabited or otherwise uninhabited sand.

A patch of sand, gravel and stones overlying clay at Area No. 71 is of interest by reason of the abundance of the anemone *Sagartia troglodytes* in the sand. Another anemone, *Tealia felina*, occurred in the gravel and stones and large blue and red specimens of *Nereis virens* in the underlying clay. Hydroids and the barnacle *Balanus crenatus* were common on the stones.

The sparsely inhabited areas of sand near Formby Point contained *Arenicola* and *Cardium* with occasionally *Chione* and *Nephthys* sp.

Except near Hoylake the shore banks on the Cheshire coast are composed of cleaner and coarser sand than on the foreshore at Waterloo and they end in the East Hoyle Bank which, in the centre, attains the considerable height of 26 ft. above Liverpool Bay datum, falling away in all directions.

A low-lying bed of mussels, *Mytilus edulis*, on shingle and stones overlying clay occurs at Area No. 47. The large areas of sparsely inhabited sand at Areas Nos. 48 and 59 contain *Cardium* and *Lanice*; these species occur in larger numbers at Areas Nos. 49 and 50. Other species include *Echinocardium*, *Macoma*, *Mactra corallina*, *Spisula solida*, *Owenia* and *Arenicola*. The last named species is common at Area No. 50 and *Owenia* is common in parts of Area No. 59. Towards the tip of the East Hoyle Bank everything except *Mactra corallina* dies away. *Lanice* and *Owenia* reappear on the Dee side of the bank and these two species also inhabit Area No. 58. *Arenicola* alone occurs at Area No. 57.

At the inshore end of the East Hoyle Bank *Corophium*, *Cardium* and *Macoma* occur in gullies at Area No. 56. *Corophium* alone occurred in great abundance at Area No. 55. A reef of rock separates Areas Nos. 55 and 54. In mud at Area No. 54 *Corophium* lived in abundance together with *Macoma*, *Cardium*, *Hydrobia* and a few *Arenicola*. In the adjoining transitional area of muddy sand at Area No. 53 *Macoma* and *Arenicola* occurred in dense, alternating patches with a few *Corophium*. *Cardium* and clumps of a seaweed *Enteromorpha* sp. were present at the Meols end of Area No. 53 with *Scoloplos armiger* and *Donax*, which two species also occurred in the adjacent part of Area No. 52. Area No. 52, of fairly clean sand, was densely inhabited by *Arenicola* which died out as the cleaner and higher centre of the bank was approached.

Only a few observations were made below low-water mark; these indicated that *Donax* was widespread and abundant in fine sand around the tip of Taylor's Bank and that *Pectinaria* was abundant in sand of a more muddy character in the channels.

Discussion

An investigation of the fauna of the estuaries of the Tees and of other rivers (*Water Pollution Research Technical Paper*, No. 5, 1935) showed that marine animals were abundant near the mouth and became less common as the estuary was ascended until eventually no marine animals were found. Similarly, the fresh-water animals, common at the head of the estuary, were found to die out as the estuary was descended.

In order to compare different estuaries the Tees Estuary was divided into thirteen sections of equal length, and comparable sections were mapped out in other estuaries on the basis of similar salinities of the water at high and low tides.

An account of the salinity conditions in the Mersey Estuary has been published (*Water Pollution Research Technical Paper*, No. 7, 1937, p. 31) so that it is possible to compare points on the two estuaries which are subject to similar salinity conditions. From such a comparison it has been found that Section XIII in the Tees (from the mouth to 1½ miles above it) corresponds in the Mersey to the whole of Liverpool Bay and part of the Narrows, and that the highest point at which collections were made in the Mersey corresponds with Section V on the Tees. From these comparisons two points emerge.

(*a*) The absence of fresh-water forms from the Mersey collections (with the possible exception of fresh-water oligochaetes) is to be expected since, in the Tees and other estuaries, fresh-water animals are only represented as low as Section V by small red oligochaetes.

(*b*) There is no reason, on grounds of differences in salinity, why the fauna of the Narrows should not be as varied as that of Liverpool Bay. Of thirty species recorded from Liverpool Bay, however, only fifteen occur in the Narrows. It seems probable that this is due to the high speed of the tidal streams in the Narrows, the large amount of sediment in the water and the relatively small area of tidal banks.

Although the salinity in the whole of Liverpool Bay is similar to that of Section XIII in the estuary of the Tees, it seemed possible that some effect of estuarine conditions might be evident near Rock Light. Accordingly the Bay was divided by a circle with a radius of 6 miles and with the centre of the channel near Rock Light as its centre. Zone A (Key Map in Plate III) within the circle is subject to the discharge of the Mersey and Alt; zone B, including the East Hoyle Bank and Spencer's Spit, might be affected by the discharge of the Dee; and zone C (Formby Point and Taylor's Bank) should be least affected by any of these discharges. A list of all recorded species for each zone shows, however, that zone C had only fourteen species, while both A and B had twenty-eight species. Any influence of the estuary which may be felt in Liverpool Bay seems therefore to have no localized adverse effect on the fauna.

Returning to a consideration of the distribution of the common burrowing animals found in the Upper Estuary it is apparent from the account given earlier in this paper that, while *Nereis diversicolor* (a brackish-water species) occurs above Hale Head, the common marine burrowing species only appear below Hale Head and do so one by one as the Estuary is descended from this point. This distribution is similar to the distribution of marine animals in the Tees and other estuaries.

Previous work on the fauna of the Mersey Estuary has been applied mainly to the bottom fauna of the Outer Estuary (e.g. Fraser, 1935). In the Upper Estuary Fraser (1938) studied the fauna of the buoys and pontoons, and he has published a detailed account of the fauna and conditions at Dingle (Fraser, 1932).

The present survey has shown that the mud banks of both the Upper and Outer Estuary are inhabited by the same species, but that the sand banks of the Outer Estuary support not only the same species as those of the Upper Estuary but in addition a large number of other species. The abundance of burrowing animals throughout the estuary is therefore due to large numbers of a few species in the Upper Estuary (notably *Nereis*, *Macoma* and *Corophium*) and in the Outer Estuary to a large variety of species. The fauna of the buoys and pontoons shows a similar distribution (Fraser, 1938, pp. 19, 20). The similarity of the mud-living fauna throughout must be attributed to the fact that few species can tolerate conditions in tidal mud flats, and that these few species are all tolerant of varying salinity conditions. Since it is only on parts of the coast sheltered from strong wave action that tidal mud banks can develop, and since such inlets are most liable to be subject to land drainage, it appears natural that an animal evolved to tolerate conditions on a tidal mud flat should also tolerate the conditions of salinity found in estuaries.

The lack of variety of sand-living species in the Upper Estuary when compared with the variety found in Liverpool Bay is probably due to intolerance of strong currents, varying salinity, and large amounts of suspended matter in the water.

Notes on the Flora

Large plants, whether marsh plants or marine algae, do not form an important feature of the Mersey Estuary. In the following list such observations as were made during the zoological survey of the tidal banks are given.

FLOWERING PLANTS

(Marsh plants or aquatic land plants)

At one time large areas of land were flooded at high water of spring tides in the Mersey Estuary. These occurred noticeably at Wallasey, Stanlow, Frodsham, Hale Head to Runcorn, and on both sides of the river just above Runcorn. The development of Wallasey Pool as a dock area and the building of the Manchester Ship Canal led to a considerable reduction in the flood areas at Wallasey, Stanlow and Frodsham, whilst much land has been protected from flooding in the other areas. There are now limited areas subject to flooding at Frodsham Score, Hale Head to Runcorn, on each side above Runcorn, and at Norton Marsh. These areas consist of coarse grassland used for grazing sheep and are cut by drainage gullies. Other marsh plants occur spasmodically in different places, but nowhere do they occupy extensive areas. Some years ago small patches of *Spartina* grass were found growing on the mud at Stanlow, and to prevent their spreading and building up the mud banks, with a consequent reduction in the capacity of the estuary, the Mersey Docks and Harbour Board destroyed the plants.

ALGAE

Fucus vesiculosus L.

Growths occur on the dock walls in the Narrows and in places on each side of the river up to Hale Head and Eastham Locks. In the Outer Estuary the only notable growths occur on the Leasowe embankment and the promenades at Meols and Hoylake.

Enteromorpha sp.

Enteromorpha occurs a little higher on the walls than *Fucus* and has a similar distribution. In addition, tufts occur on the muddy sand at Hoylake (Area No. 53).

Porphyra sp.

A small growth occurs on the rocks at Rock Ferry and in the Manchester Ship Canal.

Vaucheria sp.

Vaucheria Thuretii Woron has been identified at Dingle (Fraser, 1932), and patches—doubtless of this species—are widespread on the mud flats and near high-water mark from Dingle and Mount Manisty to Norton Marsh. Clumps and small matted growths are common on the mud at Speke (Area No. 33) and from Stanlow to the Weaver (Area No. 23).

Desmids.

Closterium sp. has been identified from below Hale Head and doubtless occurs in other localities.

Euglena sp.

The most noticeable feature of the mud banks is the presence, over extensive areas, of a bright green colour caused by immense numbers of this microscopic organism, identified at Dingle as *Euglena limosa* Gard (Fraser, 1932). It occurs from Dingle and Eastham to Norton Marsh.

Diatoms.

A brownish tinge in the green colour caused by *Euglena* is frequently observed and is due to an admixture of diatoms. Growths of diatoms, unmixed with *Euglena*, occur in places, mainly on sand.

Throughout the estuary the scarcity of rocky foreshores at low levels in the tidal zone prevents the extensive development of weed and the growth of numbers of species of animals associated with this type of habitat. The absence of weed from some areas of rock may be attributed to the film of mud covering them. In the case of the training walls flanking the main channels in Liverpool Bay the absence of large algae from what seems to be an admirable habitat may be due to the scouring action of the sand carried by the strong currents, although Fraser (1938, p. 16) attributes this absence to a reduction in illumination caused by the suspended matter.

Fauna List

All records were made between May and October 1933. Numbers refer to the Areas in the Key Map in Plate III. The names used are those of the *Plymouth Marine Fauna* (2nd edition) of the Marine Biological Association except where otherwise stated. Thanks are due to the Zoology Department of Liverpool University where some of the identifications were carried out.

COELENTERATA

Class HYDROZOA

Hydractinia echinata (Fleming).

Common on shells inhabited by hermit crabs, *Eupagurus bernhardus*. East Hoyle Bank, Spencer's Spit, Meols shore and Taylor's Bank.

Tubularia indivisa L.

Extremely abundant on the pontoons of the landing stages in the Narrows. On rocks at Gladstone Dock (71). An average of three counts of the growth on boats moored in the Narrows gave 1300 stalks of *T. indivisa* per sq. in. On one boat a growth, mainly $1\frac{1}{4}$–$1\frac{1}{2}$ in. long, had grown in 16 days and was reproducing. A count showed 1340 stalks per sq. in., of which 675 carried heads. Many heads had been knocked off in collecting and counting.

Laomedia gelatinosa (Pallas).

On Garston Rocks and on stones at Aigburth (36).

Class SCHYPHOMEDUSAE

Aurelia aurita (L).

During May and June 1933, the Upper Estuary water carried large numbers of *Aurelia aurita* and many were observed in July and August. Many stranded in May and June on the sand flats from Runcorn Gap to Dungeon Point.

Class ANTHOZOA

Tealia felina (L).

Common on stones near Gladstone dock (71).

Sagartia elegans (Dalyell) var. venusta (Gosse).

A single specimen taken near the Gladstone Dock (71).

Sagartia troglodytes (Price).

Abundant in gravel and sand near the Gladstone Dock (71).

ANNELIDA

Class CHAETOPODA

Order POLYCHAETA

Lagisca extenuata (Grube).

A single specimen at Wallasey (45).

Sigalion mathildae Audouin and Milne Edwards (Fauvel, 1923, p. 103).

A single specimen in sand on Spencer's Spit.

Nereis pelagica L.

In sand near Gladstone Dock (73), at low-water mark at Meols (51) and at Wallasey (45).

Nereis diversicolor O. F. Müller.

The commonest polychaete in the Estuary. It occurs in great abundance in the Upper Estuary from below Runcorn to Rock Ferry (7, 18, 23, 29, 33, 37, 42) and sparsely from Norton Marsh to Rock Ferry (2–5, 8–15, 17, 19, 20, 24, 26, 27, 28, 34, 38). In the Outer Estuary it is abundant in patches near the Alt (79 and 80) and occurs at 78 and 84. Usually in mud, it occurs in muddy sand (never abundantly) and occasional specimens have been taken in comparatively clean sand. These, however, may have been specimens washed out of mud which burrowed as soon as they settled.

Nereis fucata Savigny.

A single specimen from Spencer's Spit.

Nereis virens Sars. (Fauvel, 1923).

Burrowing in clay underlying sand and gravel near Gladstone Dock (71) and near Leasowe with *Pholas candida* (near 50).

Nephthys caeca (O. F. Müller).

A single specimen in sand at Spencer's Spit.

Nephthys hombergi Lamarck.

Sparsely but widely distributed in the Outer Estuary. Specimens recorded from Meols (52), Waterloo (75), near the Alt (93), Formby (89) and Taylor's Bank (97).

Nephthys hombergi var. ehlersi Heinen (Fauvel, 1923).

A single specimen from Waterloo beach in the *Arenicola* area (75).

Nephthys cirrosa Ehlers.

Single specimens obtained in sand from Wallasey (45), East Hoyle Sands (59) and Spencer's Spit.

Glycera convoluta Keferstein.

A single specimen in sand from Spencer's Spit, and one in mud at the Alt (77) with spat of *Macoma balthica* and *Cardium edule*.

Scoloplos armiger (O. F. Müller).

Common in muddy sand in a small patch at Meols (53).

Nerine cirratulus (Delle Chiaje).

Taken in sand or muddy sand at Wallasey (45), Gladstone Dock (73), Spencer's Spit and East Hoyle Sands (59).

Pygospio elegans Claparède.

Very abundant in parts of the Upper Estuary in sand (16, 17, 27 (top end near 17), 34, 35, 40, 45). Outer Estuary near the Alt (77, fringes of 80, 84, 92).

Arenicola marina L.

Sparse, but widely distributed in muddy sand in the Upper Estuary (15, 17, 22, 24, 27, 30, 32, 35, 40, 44, 45). The highest recorded specimens occurred at 15 and 22. Abundant in the Outer Estuary at Waterloo (72–75) and at Leasowe and Hoylake (50 and 52). It occurs sparsely all over the Outer Estuary (46, 48, 53, 57, 61, 62, 63, 84, 85, 86, 91, 93, 94, 96, 97) and two isolated specimens were taken on the Great Burbo Bank (69).

Owenia fusiformis Delle Chiaje.

Not taken in the Upper Estuary. Abundant in fairly clean sand in the Outer Estuary on Taylor's Bank (98, 99, 100), at Leasowe (48) and East Hoyle Sands (51, 58, 59).

Pectinaria koreni Malmgren.

Abundant in muddy sand on Spencer's Spit (60) and off Meols (51) at low-water mark. Fraser (1935) records shells of *P. belgica* at New Brighton and quotes records of *P. belgica* from Liverpool Bay.

Lanice conchilega (Pallas).

Found only on Wallasey beach (45) in the Upper Estuary. Common and widespread in sand and muddy sand in the Outer Estuary, occurring on Taylor's Bank (97), Great Burbo Bank (66, 67, 68), North Bank (63, 64), Cheshire shore banks (48, 49, 50, 51, 58, 59) and on Spencer's Spit (60, 61, 62). Not recorded from the Lancashire shore banks.

Hydroides norvegica Gunnerus.

Tubes were found on a dead shell on the East Hoyle Sands.

Pomatoceros triqueter (L).

Tubes found on the same shell as *Hydroides norvegica*.

Order OLIGOCHAETA

Clitellio arenarius O. F. Müller.

This species was identified by Fraser (1932) at Dingle (38). Small red oligochaetes occur in mud in all parts of the Upper Estuary, together with *Nereis diversicolor*, from Norton Marsh to Rock Ferry (2, 3, 18, 23, 29, 33, 37, 38, 42, 74).

ARTHROPODA

Class CRUSTACEA

Sub-class COPEPODA

Eurytemora affinis (Poppe) var. hirundoides Nordquist.

Two short plankton surveys in daylight showed this species to be present at high water in the zone above Hale Head to 2 miles above Runcorn Gap. More abundant near the bottom than at the surface.

Acartia spp.

Abundant in the plankton on two surveys to just above Hale Head. Most abundant near the bottom.

Sub-class CIRRIPEDIA

Balanus crenatus Brugière.

Fairly common on stones as far as Hale Head. Common near the Gladstone Dock (71) and on the mussels and stones at Rock Light (47). Also found on shells and stones cast up on Taylor's Bank, Spencer's Spit and the Meols shore.

Balanus balanoides (L).

Fairly common on the dock walls in the Narrows and on rocks as far as Eastham Locks. On occasional posts and rocks in the Outer Estuary.

Sub-class MALACOSTRACA

Order ISOPODA

Eurydice pulchra Leach.

Taken in clean sand on the Great Burbo Bank. Probably widespread in the Outer Estuary in similar situations.

Jaera marina (Fabricius).

Among weeds on the Garston Rocks.

Order AMPHIPODA

Gammarus marinus Leach.

Among weeds on the rocks at Rock Ferry (44).

Gammarus locusta (L).

In a pool near high-water mark at Crosby.

Gammarus duebeni Lilljeborg.

On the rocks at Garston and in gravel just above Garston (34). In pools at high-water mark just below Hale Head (near 20). Ship Canal near the Weaver.

Talitrus saltator (Montagu).

Local and widespread in clean sand at high-water mark. Found at Hale and Speke (18 and 33), Mount Manisty and Hightown.

Talorchestia deshayesei (Audouin).

A single specimen taken with *Talitrus saltator* at Hale Head.

Corophium volutator (Pallas)*.

Widespread and extremely abundant in muddy sand and mud with *Macoma balthica* and *Nereis diversicolor*. Also taken with *Arenicola marina*. Abundant at 24, 27, 42 and 44 and in parts of 23 and 29. Near high-water mark from Hale Head to Dingle (18, 33, 37). Abundant around the Alt (79, 80, 83, 84 and 95), at Hoylake (53–56) and common near the Gladstone Dock (72).

Order SCHIZOPODA

Mysids are apparently common in the Upper Estuary. Seen in abundance in shrimp nets at Garston Rocks and in a pool near Weston Locks. Taken in the plankton from Eastham to Runcorn Gap.

Order DECAPODA

Crangon vulgaris L.

The common shrimp forms the basis of a shrimp fishery, the inner grounds being fished mainly in the Eastham to Dungeon Point region, whilst shore nets are worked at and above Garston. In the Outer Estuary the main ground is the Formby Channel and along the Crosby Channel to Rock Lighthouse. The highest point at which shrimps have been observed is near the Weaver Sluices (12).

Eupagurus bernhardus (L).

Numerous specimens on the sand banks at Taylor's Bank, Spencer's Spit, East Hoyle Sands and Meols shore. Most of the shells carried a good growth of *Hydractinia echinata*.

Portunus sp.

Occasional specimens on Taylor's Bank and Spencer's Spit.

Carcinus maenas (Pennant).

Small specimens occur among rocks and gravel up to Hale Head.

Cancer pagurus L.

A specimen was taken on Taylor's Bank (97) in a pool.

Corystes cassivelaunus (Pennant).

Two females in berry were dug out of the sand near the tip of the East Hoyle Sands (59) on 20 October 1933.

MOLLUSCA

Class PELECYPODA

Mytilus edulis L.

The common mussel is abundant on buoys and pontoons in the river channels. On the shore it is abundant on the mussel bed at Rock Lighthouse (47) and at Wallasey (45); it has not been taken elsewhere. Fraser (1932) records it from Dingle.

Montacuta ferruginosa (Montagu).

Taken in the anal siphon of *Echinocardium cordatum* on Taylor's Bank (97) and Spencer's Spit (60).

---

* Identified at the British Museum (Nat. Hist.) by Dr I. Gordon.

Tellina tenuis da Costa.*

A single young elongated specimen taken in sand near low-water mark at Leasowe (48).

Macoma balthica (L.).

The commonest bivalve of the Estuary. Found in great abundance in the mud at 27 and parts of 23 and 29. It occurs in muddy sand at 24, 26, 27 and 28. Also found at 16, 17, 30, 32, 34, 35 and 43. The highest recorded specimen was taken in clean sand near 10. In the Outer Estuary it occurs in abundance at the Alt (78, 79, 80, 84) and at Hoylake (53, 54, 56), and specimens have been taken at 46, 48, 74, 75 and 94. Spat were observed at 76 and in abundance (with spat of *Cardium edule*) at 77 in mud.

Donax vittatus (da Costa).

Found in extreme abundance on Spencer's Spit (61) at low water of spring tides. It also occurs at 52, 60 and 101. On Spencer's Spit small clusters of whole and broken specimens seemed to indicate that the gulls flocking on this bank were feeding to repletion and then regurgitating. The area is exposed only at spring tides.

Mactra corallina (L.).

Found in sand near low-water mark. Large specimens were sparsely distributed over the tip of the East Hoyle Sands (59). Broken shells indicated that gulls had been feeding on them. Smaller specimens were obtained along the Meols shore (51 and 48) and as far as Leasowe.

Spisula solida (L.).

Occasional on the East Hoyle sands (59) and near Leasowe (48).

Chione striatula (da Costa).

Nowhere abundant but widely distributed in the Outer Estuary. Recorded from Taylor's Bank (97), Formby shore (87 and 88) and North Bank (63, 64, 65).

Cardium echinatum L.

Dead shell picked up on the East Hoyle Sands (59).

Cardium edule L.

Common in the Outer Estuary. Abundant on Taylor's Bank (97) and common along the Leasowe shore (48, 49, 50) and at Hoylake (53, 54, 56). It occurs sparsely at 71, 85, 86, 89 and 96. Young specimens were abundant at 77 and 92. In the Upper Estuary they are found at Dingle (38) where dwarfing is apparent (Fraser, 1932).

Cardium rusticum L. (Forbes & Hanley, 1853, Vol. II, p. 11).

Dead shells are common along the Leasowe shore and at the Gladstone Dock. A few specimens occur on Taylor's Bank (97) among *C. edule*.

Mya arenaria L. (Forbes & Hanley, 1853, Vol. I, p. 168).

A large patch of small specimens occurs in mud near Stanlow (25). The species also occurs at Dingle (37, 38) where dwarfing is again apparent (Fraser, 1932). At Rock Ferry (43) the specimens are larger than at 25; in localized but abundant patches of very muddy sand at 51 off Meols, still larger specimens occur. These last, however, are considerably smaller than the dead shells common along the Hoylake and Meols shore.

---

* Identified at the British Museum (Nat. Hist.) by Mr G. C. Robson.

Mya truncata L.

A dead shell was picked up on the Meols shore (59).

Ensis siliqua (L.).

A few young specimens were dug in muddy sand off Meols (51).

Ceratisolen legumen L. (Forbes & Hanley, 1853, Vol. I, p. 256).

A single living specimen was taken on Spencer's Spit (60) although dead shells are common along the Leasowe shore (49).

Pholas candida L. (Forbes & Hanley, 1853, Vol. I, p. 117).

Outcrops of clay occur in the sand in many parts of the estuary. At Moreton and Leasowe several patches at about half tide level are inhabited by small specimens of *Pholas candida*; large dead shells are abundant along the Leasowe shore (49, 50) and may be picked up anywhere in the Outer Estuary.

Class GASTROPODA

Littorina littorea (L.).

The periwinkle has been found on stones at Wallasey (45), Rock Ferry (43) and at Dingle (37 and 38). It is extremely abundant in patches.

Hydrobia ulvae (Pennant).*

This small snail occurs on the surface of sand or mud over wide areas at the Gladstone Dock (72 and 73), Waterloo (74 and parts of 75), Hightown (84) and Hoylake (53 and 54). It also occurs in vast numbers in long pools behind the Leasowe Embankment. In the Upper Estuary it has been recorded from Dingle beach by Fraser (1932).

Natica nitida Donovan (Forbes & Hanley, 1853, Vol. III, p. 330).

Rare. Taylor's Bank (97).

Tornatella fasciata L. (Forbes & Hanley, 1853, Vol. III, p. 523).

Occasional. Taylor's Bank (97).

Aeolidiidae.

Numerous Eolids were found spawning on slag on Taylor's Bank (97) (27 Aug. 1933) and feeding on *Tubularia indivisa* at Gladstone Dock (71).

ECHINODERMATA

Class OPHIUROIDEA

Ophiura texturata Lamarck.

A few specimens were observed near low-water mark off Meols (51). On Spencer's Spit the species was widely distributed near the centre of the bank. Numerous in patches in which the specimens formed a carpet over the surface of the sand. In an area of roughly 15 sq. yd. a count of the numbers in $\frac{1}{4}$ sq. ft. indicated that there were 20,400 individuals in the patch (1400 per sq. yd.). Many similar patches occurred.

Class ECHINOIDEA

Echinocardium cordatum (Pennant).

Abundant on Taylor's Bank (97) and Spencer's Spit (60 and 61). Less common at 62 and 51. Also found at 59 and 48 near low-water mark.

---

* Identified at the British Museum (Nat. Hist.) by Mr H. M. Tomlin.

BRYOZOA

Class ECTOPROCTA

Triticella pedicillata Alder (Hincks, 1880, p. 547).

Common in pools near Mount Manisty (near 32) apparently broken off from the Dolphin piles at Eastham where the growths of this species are abundant.

SUMMARY

The 37 sq. miles of intertidal banks in the Mersey Estuary have been surveyed and classified according to their nature and fauna.

Half the banks occur in the Outer and half in the Upper Estuary. Four-fifths of the total area is composed of sand and most of the remaining one-fifth of mud occurs in the Upper Estuary.

The burrowing fauna of the Outer Estuary is abundant and varied; that of the Upper Estuary is abundant but not varied.

The distribution of species in the Mersey Estuary is similar to that in the estuaries of the River Tees and Tay, except that in the Mersey Estuary a sudden drop in the numbers of species occurs at Rock Light. This is attributed to the strong tidal streams in the Narrows.

The densely inhabited banks of the Upper Estuary are mainly composed of mud and are situated high in the shore zone. In the Outer Estuary the densely inhabited banks are of muddy sand with some banks of mud and are situated near the low-water mark in sheltered positions.

The burrowing species of the Upper Estuary also occur, with many others, in the Outer Estuary.

The observations described in this paper were made during an investigation of the estuary of the River Mersey by the Water Pollution Board of the Department of Scientific and Industrial Research and the results are published by permission of the Department.

REFERENCES

Fauvel, P., 1923. Polychètes Errantes. *Faune de France*, Vol. 5.

Forbes, E. & Hanley, S., 1853. *A History of British Mollusca and their Shells.* London. Vols. I–IV.

Fraser, J. H., 1932. Observations on the fauna and constituents of an estuarine mud in a polluted area. *Journ. Mar. Biol. Assoc.*, N.S., Vol. XVIII, p. 69.

—— 1935. The fauna of the Liverpool Bay Shrimping Grounds and the Morecombe bay Prawning Grounds as revealed by the use of a beam trawl. *Proc. Trans. Liverpool Biol. Soc.*, p. 65.

—— 1938. The fauna of fixed and floating structures in the Mersey Estuary and Liverpool Bay. *Proc. Liverpool Biol. Soc.*, Vol. LI, pp. 1–21.

Ghazzawi, F. M., 1933. The littoral diatoms of the Liverpool and Port Erin shores. *Journ. Mar. Biol. Assoc.*, Vol. XIX, p. 165.

Hincks, T., 1880. *British Marine Polyzoa.* London.

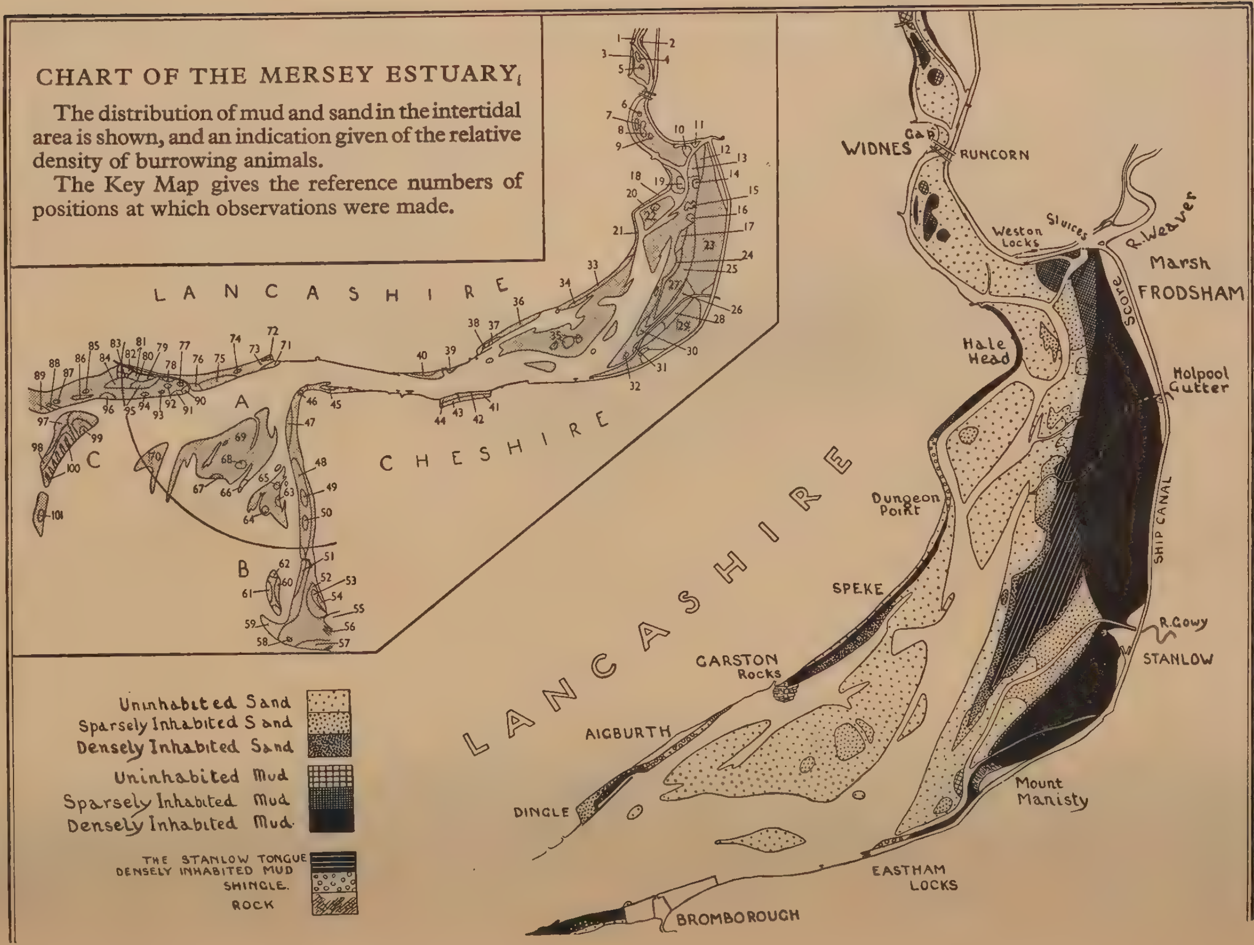
Water Pollution Research, 1935. Alexander, W. B., Southgate, B. A. and Bassindale, R. Survey of the River Tees. Part II. The Estuary—Chemical and Biological. *Dept. Sci. Indus. Res.*, Water Pollution Research Technical Paper, No. 5. H.M. Stationery Office.

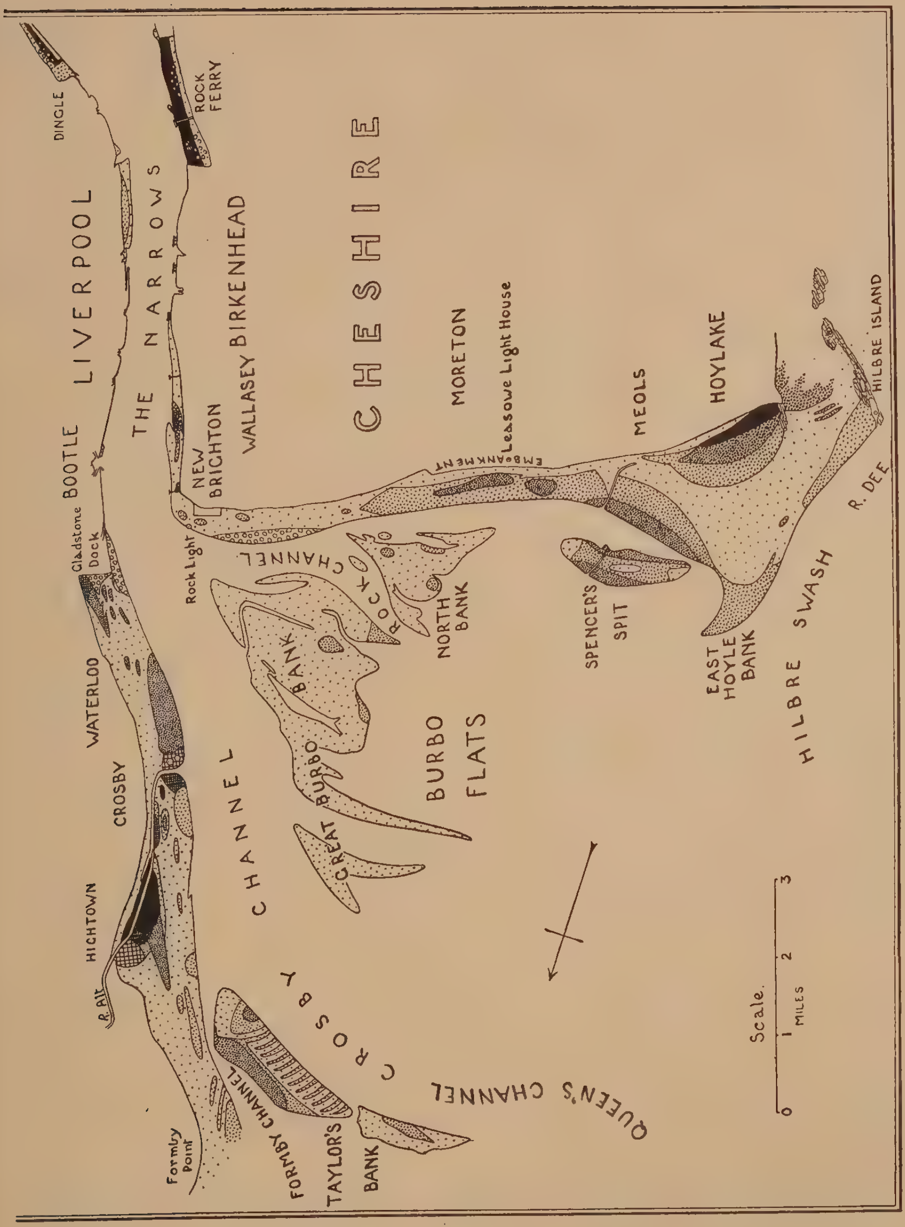
—— 1937. Effect of discharge of crude sewage into the estuary of the River Mersey on the amount and hardness of the deposit in the Estuary. *Dept. Sci. Industr. Res.*, Water Pollution Research Technical Paper, No. 7. H.M. Stationery Office.

CHART OF THE MERSEY ESTUARY

The distribution of mud and sand in the intertidal area is shown, and an indication given of the relative density of burrowing animals.

The Key Map gives the reference numbers of positions at which observations were made.


LANCASHIRE
CHESHIRE
A
B
C
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100 101
Uninhabited Sand
Sparsely Inhabited Sand
Densely Inhabited Sand
Uninhabited Mud
Sparsely Inhabited Mud
Densely Inhabited Mud
THE STANLOW TONGUE DENSELY INHABITED MUD
SHINGLE.
ROCK
WIDNES
Gap
RUNCORN
Weston Locks
Sluices
R. Weaver
Marsh
FRODSHAM
Score
Hale Head
Holpool Gutter
Dungeon Point
SHIP CANAL
SPEKE
LANCASHIRE
R. Gowy
STANLOW
GARSTON Rocks
AIGBURTH
Mount Manisty
DINGLE
EASTHAM LOCKS
BROMBOROUGH


DINGLE
ROCK FERRY
LIVERPOOL
THE NARROWS
BIRKENHEAD
WALLASEY
CHESHIRE
BOOTLE
NEW BRIGHTON
MORETON
Leasowe Light House
EMBANKMENT
MEOLS
HOYLAKE
HILBRE ISLAND
Gladstone Dock
Rock Light
ROCK CHANNEL
NORTH BANK
SPENCER'S SPIT
EAST HOYLE BANK
R. DEE
HILBRE SWASH
WATERLOO
CROSBY
BURBO BANK
BURBO FLATS
GREAT BURBO
CHANNEL
HIGHTOWN
R. Alt
CROSBY
Formby Point
FORMBY CHANNEL
TAYLOR'S BANK
QUEEN'S CHANNEL
Scale.
0
1
2
3
MILES

THE PHOTOGRAPHIC METHOD FOR RECORDING AVERAGE ILLUMINATIONS

By L. E. Bayliss, B.A., Ph.D.

Department of Physiology, University of Edinburgh, and the
Marine Biological Laboratory, Plymouth

(Text-figs. 1–3)

The photo-electric cell is admirably suited for measuring instantaneous illuminations, but does not lend itself readily to the measurement of the total illumination received on a surface over a long period of time, or the average illumination received during that time, although it has been used for this purpose (Atkins & Poole, 1936*a*). The method used by these authors, however, would be difficult to use in the field and away from laboratory facilities. The photographic method, on the other hand, is admittedly not capable of yielding results of high precision, but the simplicity of operation, and absence of elaborate and bulky apparatus, make it suitable for use in the field.

In principle, the amount of blackening produced in a photo-sensitive emulsion is used as a measure of the total illumination received; in order to increase the range over which measurements can be made, a neutral tint wedge, of suitable slope, is placed in front of the emulsion, and the distance along the wedge at which a standard amount of blackening is produced is taken as a measure of the illumination. The standard amount of blackening is best defined as that amount which is produced, in the absence of the wedge, by a known illumination acting for a known time. The method has inherent limitations, particularly when used for long-period observations, which result from (*a*) the failure of the reciprocity law, (*b*) the uncertainty in the value of the wedge constant, and (*c*) the varying sensitivity of the emulsion to lights of different wave-lengths.

The use of the neutral tint wedge in photometry has been fully described by Hecht (1918) and Eder (1919, 1920*a*, *b*). These authors, however, do not appear to have considered in any detail the possible effects of the limitations just mentioned, although their existence is recognized. Gruber (1924) and Oberdorfer (1928) used the Eder-Hecht photometer for ascertaining the intensity of illumination at various depths below the surface of a lake, and Cooper & Sayce (1932) made continuous records of the intensity of daylight throughout the day, with the aid of a neutral tint wedge. Such observations, however, fail to make use of the innate integrating properties of the photographic emulsion.

Let the emulsion be exposed behind the wedge to a constant illumination I for a time t. Let the print of the wedge at a distance l from the zero end of the wedge have the same density (amount of blackening) as that produced by the standardizing light, of intensity I_s acting for the same time, t. Then the intensity of light actually reaching the emulsion must be the same during both exposures. Now, if $I^\star$ is the intensity of light emerging from the wedge, and striking the emulsion, we can write, from the known properties of the wedge,

$$\log I^\star = \log I - kl,$$

where k is the "wedge constant". Hence, in the particular case considered,

$$\log I = \log I_s + kl.$$

If, however, the duration of the standardizing exposure is not the same as that of the wedge exposure, or if the intensity of the illumination during the latter is not constant, complications arise.

THE FAILURE OF THE RECIPROCITY LAW

The total illumination received during any time t is given by $R = It$, if the intensity is constant. The amount of blackening produced in a photographic emulsion, however, by a constant illumination acting for a time, t, does not, in general, follow this "reciprocity law", but depends upon the product It^p, where p is the "Schwarzschild constant" (Schwarzschild, 1900). If, as before, $I^\star$ is the illumination actually reaching the emulsion, during the wedge exposure, at the point l, as previously defined,

$$R^\star = I^\star t,$$

whence $$\log R = \log R^\star + kl.$$

But at the point l the amount of blackening produced under the wedge is the same as that produced by the standardizing exposure of intensity I_s and of duration t_s. We can write, therefore,

$$I^\star t^p = I_s t_s^p$$

or $$R^\star t^{p-1} = R_s t_s^{p-1},$$

whence $$\log R = \log R_s + kl + (p-1)\log(t_s/t).$$

An extensive treatment of the law of blackening of the photographic emulsion, and the failure of the reciprocity law, is given in the monograph by Dobson, Griffith & Harrison (1926).

Clearly, then, a correction must be introduced whenever the standardizing exposure and the wedge exposure are of different durations, unless the value of p approximates sufficiently closely to unity.

TABLE I. CORRECTION TO BE APPLIED TO PHOTOGRAPHIC RECORDS DUE TO DEPARTURE FROM THE RECIPROCITY LAW

	t_s/t				
p	0·1	0·2	0·3	0·5	0·7
1·03	0·935	0·95	0·965	0·980	0·990
1·05	0·890	0·92	0·935	0·965	0·980
1·10	0·790	0·85	0·885	0·930	0·965

Values of this correction are given in Table I. Two points are of significance in connexion with these figures. (*a*) In many cases, the total illumination received over the whole period of daylight must be measured, while it is inconvenient to continue the standardizing exposure for more than 1 or 2 hr. (*b*) In such cases, the exact duration of the illumination under measurement is difficult, or impossible, to discover; this is usually of no importance, except that the exact value of the correction to be applied is also unknown, and so must be kept small. It will be shown in a later section that the inherent experimental uncertainty of the method is about ±10%. The maximum tolerable departure of the value of p from unity is thus about ±0·05.

Non-uniform illumination. The magnitude of the correction necessary when the illumination is fluctuating depends, obviously, on the nature of the fluctuation. Two special cases, however, may be considered.

(1) The exposure is made on a clear day from sunrise to sunset, so that we may write, approximately,

$$I = I_0 \sin \frac{\pi t}{12},$$

where t is the time in hours. The total radiation received is thus

$$R = \int_0^{12} I_0 \sin \frac{\pi t}{12}\, dt = \frac{24}{\pi} I_0.$$

The amount of blackening produced, however, depends upon the quantity S, where

$$S = \int_0^{12} \left(\frac{\partial S}{\partial t}\right) dt = \int_0^{12} p t^{p-1} I_0 \sin \frac{\pi}{12} t\, dt.$$

Graphic integration of this expression, putting $p = 1{\cdot}10$, gives

$$S = 10{\cdot}1\, I_0.$$

We will assume, for simplicity, that the standardizing exposure has the same duration as the wedge exposure, hence

$$S_s = (12)^{1{\cdot}10}\, I_s = 15{\cdot}4\, I_s.$$

Similarly $$R = \frac{24}{\pi} I_0,$$

$$R_s = 12\, I_s.$$

If the amount of blackening produced in the two exposures is the same, then $S = S_s$, and

$$I_0 = \frac{15{\cdot}4}{10{\cdot}1} I_s = 1{\cdot}53\, I_s.$$

The fact that the unknown exposure produced the same amount of blackening as the standardizing exposure, however, would lead us to suppose that the total radiation received in both cases was the same, i.e. that

$$R_s = 12\, I_s = R_0 = \frac{24}{\pi}\, I_0$$

or that

$$I_0 = 1{\cdot}57\, I_s.$$

The estimate of the total illumination received, in terms of the amount of blackening produced, will thus be too high by about 3%.

(2) The illumination is fluctuating in a simple harmonic fashion about a fixed value. This approximates to the conditions in the neighbourhood of noon, with intermittent clouds. The intensity at any moment can now be written,

$$I = I_1 + I_2 \sin \omega t.$$

Since the greatest fluctuations, and hence the greatest possible discrepancy, will be when the illumination falls periodically to zero, we can simplify the expression, and write

$$I = I_0\, (1 + \sin \omega t)$$

and

$$R = I_0 \int_0^t (1 + \sin \omega t)\, dt.$$

If t is such as to occupy any whole number of waves, this reduces to $R = I_0 t$, i.e. the fluctuations do not affect the total illumination received.

Similarly

$$S = pI_0 \int_0^t t^{p-1}\, (1 + \sin \omega t)\, dt$$

$$= I_0 t^p + pI_0 \int_0^t t^{p-1} \sin \omega t\, dt.$$

The second term in this expression has the property that the area of any half-wave is greater than the area of the preceding half-wave. The area of successive whole waves, however, approaches zero as t becomes greater, so that the area of the first whole wave will give a measure of the maximum discrepancy introduced, which will not be exceeded however many subsequent waves are included in addition. Since, in general, any type of fluctuation can be reduced to a series of simple harmonic waves of suitable frequency, this discrepancy must also be the maximum which will be introduced by any type of fluctuation about a finite mean.

Graphic integration, with $p = 1{\cdot}10$ as before, over the first complete wave gives $I_0 = 1{\cdot}04\, I_s$ as the condition that the same amount of blackening shall be produced by the fluctuating light as by the standardizing light. We should be led to believe, however, that $I_0 = I_s$, and the discrepancy introduced is thus about 4%. The photographic measure of the illumination will be smaller or greater than the true measure according as the exposure was begun while the illumination was rising or falling.

In general, then, fluctuations in the illumination will not introduce any discrepancy greater than 2 or 3 % so long as the Schwarzschild constant does not differ from 1 by more than 0·10.

The Wedge Constant

The wedge was of the Goldberg (1910) pattern and was supplied by Messrs Ilford, Ltd. It was 21 cm. long by 1·25 cm. wide, with a density of 3·0 at the dense end and was cut in the middle, the two halves being mounted side by side so as to form a rectangle 10·5 × 2·5 cm.; a wide range of densities was thus available in a compact form. The wedge itself was mounted between two pieces of glass, one of which was made as thin as possible (1 mm.) in order to reduce the shading effect of the edges, and the errors introduced by parallax between the wedge and the paper.

The makers of the wedge furnish a figure for the relation between the density of the wedge at any point, and the distance of this point from the end of the wedge; this is derived from measurements made in the photometer described by Benson, Ferguson & Renwick (1918) and will not necessarily be applicable in all circumstances. The disturbing factors are (1) the inclination of the incident light to the normal, and (2) the wave-length sensitivity of the photo-sensitive material with which the wedge is used. The first arises from the fact that a ray of light passing through the wedge obliquely has to traverse a greater thickness of absorbing material than one passing through normally. The second arises from the fact that the material of which the wedge is composed, while strictly "neutral" in that the density at any point is independent of the wave-length for all values greater than about 420 mμ, becomes rapidly denser with decrease in wave-length below this figure, as has been shown by Toy & Ghosh (1920). In the Ferguson-Benson-Renwick photometer, the wedge is illuminated by diffuse light and the densities are measured visually, so that the effective wave-length is considerably larger than 420 mμ.

The Effect of the Inclination of the Incident Light

If the wedge is illuminated by light derived from a diffusing surface, which is itself illuminated by approximately parallel light incident nearly normally, the conditions will be identical with those in which it is calibrated, and the makers' figure may be used. It is of interest, however, to investigate what corrections would be needed in the following circumstances. (1) The degree of imperfection of the diffusing surface used differs from that of the diffuser used by the makers (a "perfect" diffusing surface is considered to be one from which the illumination emitted per unit solid angle is independent of the direction of emission, i.e. the illumination emitted per unit area is proportional to the cosine of the angle of emission). (2) Parallel light is incident obliquely on an imperfect diffusing surface. (3) Parallel light is incident obliquely on the wedge without interposition of a diffusing surface. (4) The wedge is illuminated by the system of two lamps and diffusing surface used in the measurement of the Schwarzschild constant (see below).

(1) *Calculation of the ratio of the wedge constant in diffuse light to that in parallel light.* Let the wedge be illuminated by an infinite diffusing surface. Consider the illumination received by any point on the wedge from an elementary annulus which subtends an angle θ at this point. Let the illumination emitted per unit solid angle be I_θ. I_θ is a measure of the imperfection of the diffusing surface, and is independent of θ if the illumination is perfectly diffuse. Then, the illumination emitted per unit surface in the direction θ is $I_\theta \cos\theta$.

The total illumination received at the point considered from the elementary annulus is $2\pi I_\theta \sin\theta\, d\theta$, and the vertical component is $2\pi I_\theta \sin\theta \cos\theta\, d\theta$. The total illumination falling on the wedge $= I = \int_0^\pi 2\pi I_\theta \sin\theta \cos\theta\, d\theta$. This expression reduces to πI_θ for perfectly diffuse light, and can be evaluated graphically if the relation between I_θ and θ is determined empirically for any given diffusing surface. But this illumination passes through the wedge at an angle ϕ, where $\sin\theta/\sin\phi = \mu$, the refractive index of the material of which the wedge is composed. Hence, if D is the density of the wedge at the point considered to light of normal incidence, the density to light incident at an angle θ is $D/\cos\phi$, and the vertical component transmitted is

$$\frac{2\pi I_\theta \sin\theta \cos\theta\, d\theta}{(10)^{D/\cos\phi}}.$$

The total illumination received on the paper after passing through the wedge is thus

$$\int_0^\pi \frac{2\pi I_\theta \sin\theta \cos\theta\, d\theta}{(10)^{D/\cos\phi}} = I^\star.$$

Integration can again be carried out graphically. The effective density of the wedge to light emitted from any given diffusing surface is given by $\log_{10} I^\star/I = D'$. For perfectly diffuse light, the ratio D'/D was calculated to be 1·135, while for light from two samples of surface-flashed opal glass, the ratio D'/D was found to be 1·120 and 1·125 respectively; the second of these was markedly more nearly "perfect" than the first. μ has been taken as 1·5, a value which is probably rather too large.

The "imperfection" of an actual diffuser was measured by projecting an image of an incandescent filament 2 mm. wide normally on one side; the intensity of the light emitted on the far side at a number of angles to the normal was then measured by means of a rectifier photo-cell behind a slit 2 mm. wide, and 45 mm. from the diffuser. The photo-cell and galvanometer used were calibrated by means of an inverse square law photometer.

It would appear that variations in the "perfection" of the diffuser over reasonable limits will not seriously affect the value of the wedge constant.

Atkins & Poole (1936*b*) remark that "a 1 mm. filter is about equivalent to a similar one 1·15 mm. thick, if it is used in diffuse light". The calculated figures are in adequate agreement with this observation.

(2) *The effect of parallel light incident obliquely on an imperfect diffuser.* In this case, the illumination emitted by the elementary annulus will not be uniform at all points, but will reach a maximum in the direction of the incident light. The distribution of intensity of the light emitted was measured by projecting the image of the incandescent filament on the diffusing surface at an angle to the normal, either in the plane of rotation of the photo-cell, or in a plane at right angles. From the approximate distribution curve so obtained, the mean circular intensity was derived, and used as the value of I_θ in the expression given in the previous section. For an angle of incidence of 60°, and the less perfect diffusing surface, the value of D'/D so obtained was 1·14. The distribution curve was very little affected by further increase in the angle of incidence, so that we may take it that for this particular diffusing surface, the value of D'/D would lie between 1·12 and 1·14 for all angles of incidence. Further, the figures are not likely to be altered significantly by considerable changes in the degree of imperfection of the diffusing surface.

(3) *Parallel light is incident obliquely on the wedge without the interposition of a diffusing surface.* Here, $D'=D/\cos\phi$, where $\sin\theta/\sin\phi=\mu$. If μ is taken as 1·5, the values given in Table II are obtained. In actual practice, however, if a wedge is exposed to bright sunlight, the value of D'/D will not vary to so great an extent with the altitude of the sun. In the first place, there is a considerable amount of scattering of light within the wedge itself, with the result that the observed value of D'/D for an imperfect diffuser was $1{\cdot}09 \pm 0{\cdot}02$ instead of the calculated 1·12. In the second place, the wedge is never exposed to pure sunlight, but to a mixture of sunlight and diffuse skylight. Atkins & Poole (1936*a*) give a large number of values for the ratio of the vertical component of sunlight to the vertical component of skylight, from which average values can be obtained for various altitudes of the sun. The estimated actual values of D'/D for sunlight + daylight are given in the last line in Table II. In addition, if a wedge recorder is exposed at sea, the random motion will largely average out the values of D'/D. The average of the figures for pure sunlight given above is 1·15, a value which differs little from that for diffuse light.

TABLE II. RELATIVE VALUES OF WEDGE CONSTANT IN LIGHTS OF VARYING OBLIQUITY

Angle of incidence	0°	30°	45°	60°	90°
D'/D calc.	1·00	1·06	1·135	1·22	1·34
D'/D daylight conditions	—	1·10	1·135	1·16	—

A second-order effect on the wedge constant produced by light incident obliquely in the plane of the long axis of the wedge arises from the fact that light reaching the photo-sensitive surface at a point distant l from the zero end of the wedge, will pass through the wedge at some point distant $l \pm \Delta l$ from the zero end. If d is the thickness of the glass between the wedge and the photo-sensitive surface, $\Delta l = d \tan \phi$. Now the maximum value of ϕ is $\sin^{-1} \mu$, where μ is the refractive index of the glass. If this is taken as 1·5, the maximum value of Δl, for $d = 1$ mm., becomes 0·9 mm., corresponding to a maximum increase or decrease in density of 3 %. This effect, of course, will not be apparent in diffuse light, since the positive and negative corrections will be equal.

It is clear, therefore, that it is always advisable to place a sheet of diffusing material above the wedge. The extra uncertainty introduced by the omission of the diffuser, however, is not likely to be large except when the recorder is exposed on land to bright sunlight with the altitude of the sun greater than about 55° or less than about 35°. If the diffuser is used, care must be taken that the diffusing surface is large enough to allow the intensity of illumination at the ends of the wedge to be the same as that in the centre. It can easily be shown that the necessary minimum length of a perfect diffusing surface increases as its distance from the wedge increases. If the wedge is 10 cm. long, and the diffusing surface is 5 cm. from it, and 25 cm. long, the intensity at the ends of the wedge will be 3 % less than that at the centre. If, on the other hand, the diffusing surface is only 0·5 cm. from the wedge, a 3 % difference of intensity will be obtained with a diffusing surface only 11 cm. long. In both cases the illumination sensibly reaches the value at the centre at points 0·5 cm. from the ends.

It may be pointed out that any uncertainty in the value of the wedge constant only becomes significant if the illumination integrals to be compared differ considerably in magnitude. Thus while it may not be possible to determine with great accuracy the absolute value of, say, the total illumination received during one day, it is possible to compare this illumination with that received during another day with considerable accuracy.

(4) *The constant of the wedge when exposed to the source of light used for the measurement of the Schwarzschild constant.* The value was found by direct measurements to be identical with that for diffuse light, except when measurements were made at points immediately opposite one of the lamps. As was to be anticipated, owing to the imperfection of the diffusing arrangements, the wedge constant at these points was lower than at other points—actually by about 3·5 %. This discrepancy is of no consequence, as the extreme ends of the wedge were always placed opposite the lamps, and no measurements were made on the corresponding parts of the prints.

The Effect of the Wave-length of the Light

The particular wedge examined by Toy & Ghosh (1920) had a density at 300 mμ. which was 2·2 times the density at 420 mμ. Now the photographic emulsion is mainly affected by light of short wave-lengths, and it is thus clearly necessary to inquire whether it is appropriate to use the "visual" wedge constant when calculating the effective intensity of light falling on the photographic paper.

In the case of gaslight paper, it is possible to determine the "photographic" wedge constant directly. The paper is exposed behind the wedge on a number of occasions for the same duration, but at different distances from a point source of light. If precautions are taken to avoid stray light, the inverse square law can be applied, and the wedge constant determined by the inverse of the method used to determine the intensity of an unknown illumination, as described above.

An automobile head-lamp bulb was used as source of light, and exposures were made at distances varying from 50 to 400 cm. The values obtained for the wedge constant were independent of the distance from the source of light, indicating the validity of the inverse square law, and the mean "photographic" value, so determined, was 38% higher than the "visual" value for parallel light as measured by a rectifier type photo-cell; the correction, therefore, is clearly of great importance.

Unfortunately, it is hardly possible to make similar direct measurements with "P.O.P.", owing to the difficulty of obtaining a point source of light sufficiently intense to allow of reasonable durations of exposure. An estimate of the probable magnitude of the correction, however, can be obtained from the spectral sensitivity curves of the emulsion before and after interposing the wedge between the source of light and the spectrograph; details of the methods used are given in a later section. The curves are shown in Fig. 2. If A_0 and A_w are the areas below the curves obtained in the absence of the wedge, and in its presence, respectively, then it can be shown that $D' = \log A_0/A_w$, where D' is the "photographic" density of the wedge at the point used. For "Slogas" the photographic density calculated in this way agreed within the limits of error with that determined directly. No very great accuracy can be expected, since the result depends considerably on the value chosen for the Schwarzschild constant.

It was not possible to obtain a spectral sensitivity curve for P.O.P. with the wedge in position owing to the very long exposures that would have been necessary. The curve can, however, be constructed, since the density of the wedge for any given wave-length is known from the observations on the gaslight paper. The photographic density is thus found to be 3% greater than the visual density, when tungsten filament light was used. For sunlight and daylight the corresponding corrections are 2 and 4% respectively.

CHOICE OF EMULSION

For general reasons, a relatively insensitive emulsion that requires the least amount of processing is desirable, and P.O.P. and gaslight paper appear to be the most suitable. A paper support for the emulsion also has some advantages over celluloid or glass. As there appear to be no records in the literature of measurements of the degree of failure of the reciprocity law in these emulsions, or of the spectral sensitivity of P.O.P., such measurements have had to be made.

The Applicability of the Reciprocity Law to P.O.P. and Gaslight Paper

The paper was exposed behind a neutral tint wedge to a uniform source of light for different times. In general, four exposures were made on each sheet of paper, of approximately 1, 3, 8 and 24 hr. respectively. The prints were processed in the usual way, and dried. The method was sensibly the same as that described by Mallett (1922, 1923). Two millimetres were then trimmed off the sides of each wedge print, in order to eliminate the effects of shading by the binding of the wedge, and two of the four strips so formed were placed beneath a slit 2 mm. wide in a piece of cardboard. One strip was then fixed so that the portion of the print beneath the slit was of a suitable density, and the other slid longitudinally until it also had the same density. Four such density matches were made, and then the two strips reversed in position, so as to eliminate as far as possible the effects of uneven illumination, accidental irregularities in the paper, and so forth, and four more matches made. The mean of the eight readings was then taken. If l_1 is the distance from the slit to the end of the print, corresponding to the zero end of the wedge, on the first strip, and l_2 the corresponding distance on the second strip, then, from the equation for the blackening of a photographic emulsion, given above,

$$\log I - kl_1 + p \log t_1 = \log I + kl_2 + p \log t_2,$$

where I is the intensity of the illumination during the exposure. Hence

$$p = \frac{k\,(l_1 - l_2)}{\log\,(t_1/t_2)}.$$

The comparison can, of course, be made at any desired density of the wedge prints, and, in general, four different densities were used whenever possible, defined arbitrarily as "very pale", "pale", "medium" and "dark". Such comparison at several different densities assists in eliminating the well-known unevenness in the response of different parts of the same emulsion. The use of a paper support, moreover, reduces this unevenness considerably, by allowing the processing solutions to reach the emulsion from both sides.

The Source of Light. It was necessary to obtain sensibly uniform illumination over a length of 10 cm. (about 3 mm. at each end of the wedge print were rejected in any case, owing to the shading by the binding which held the wedge between the glass plates), of sufficient intensity to produce an adequate density in the print in 1 hr., and free from random fluctuations over a period of at least 24 hr. Spatial uniformity was obtained in the case of gaslight paper by placing the wedge and paper a sufficient distance from the source of light, which was a 12 V. 36 W. automobile head-lamp bulb. A distance of

2·5 m. was found to give a suitable intensity. For P.O.P. a much greater intensity is required, and two such head-lamp bulbs were used, mounted about 10·5 cm. apart, and with a sheet of surface flashed glass in contact with the bulbs. The wedge and paper were then mounted as close as was possible without introducing sensible non-uniformity of the illumination; this was about 7 cm. from the lamp filaments. The uniformity of illumination was checked at intervals by means of a rectifier type photo-cell, and slight adjustments made if necessary. The two lamps usually had surprisingly equal emissions, but any small difference was eliminated by bringing one lamp closer to the wedge than the other.

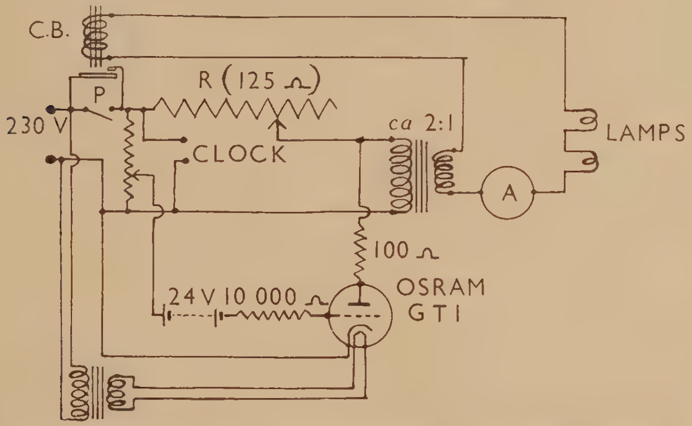


Fig. 1. Diagram of circuit used for current stabilization in lamps used as source of illumination. *R*, main voltage dropping resistance; *P*, bell-push for starting current through lamps; *CB*, no-load circuit breaker.

Temporal uniformity was obtained by running the lamps off the A.C. mains in conjunction with one of two types of current stabilizer. The first involves the use of a gas-filled relay (or thyratron—for characteristics, see Hull, 1929), and the circuit is shown in Fig. 1. If the line volts rise, the negative bias on the grid of the relay falls more during each positive half-wave, and the current taken by the relay rises more than in proportion to the rise in the line volts. The potential drop across the resistance *R* is increased, and the volts fed to the transformer, and hence the current in the lamps is reduced. A no-load circuit breaker was included as subsidiary equipment. If the current through the lamps fails, either through failure of the supply, or breakage of a filament, the circuit-breaker *CB* opens, and protects the gas-filled relay from the rise of anode potential that would otherwise follow. The circuit-breaker cannot be closed again except by deliberately closing the bell-push *P*. The current regulation obtained was such that a 1% change in the lamp current was produced by a 5% change in the line volts; considerably better regulation was obtained for smaller changes in the line voltage. The G.T. 1 gas-filled relay does not take quite a large enough anode current for perfect regulation; in particular, occasional large mains fluctuations would extinguish it entirely. It would have been better to have included a step-up transformer in front of the circuit shown, so that a larger value of *R* could have been used.

The second type of current stabilizer used depended upon the action of a barretter. Two type 304 Osram barretters were used in parallel, in the primary circuit of a Zenith regulating transformer, together with a variable resistance and the no-load circuit breaker, the lamps being connected in the secondary circuit. When two lamps were being used, it was necessary to step up the supply to about 350 V., in order to bring the barretters to the proper operating conditions. The degree of regulation obtained was rather better than with the circuit shown in Fig. 1 for slow fluctuations, a 1 % change in lamp current being produced by a 10 % change in line voltage. Owing to the slow response of the barretters, however, they were unable to take charge of rapid fluctuations.

In both circuits, an electric clock was connected in the circuit beyond the no-load circuit-breaker. This indicated the duration of the exposure in the event of the circuit-breaker opening for any reason.

The Value of the Schwarzschild Constant

A. *P.O.P.* (*Ilford matt white*). Seventeen experiments were performed involving sixty-eight exposures and 124 determinations of the Schwarzschild constant. The results are shown in Table III. Previous to these, ten experiments had been performed while the technique was being developed. The results of these were more erratic, but the general conclusions to be drawn are the same.

TABLE III. THE SCHWARZSCHILD CONSTANT FOR P.O.P.

Duration of exposure, hr.	Density of print			
	Very pale	Pale	Medium	Dark
1–3	1·05 ± 0·023	1·02 ± 0·013	1·04 ± 0·012	—
3–8	1·04 ± 0·033	1·03 ± 0·022	1·00 ± 0·020	0·83 ± 0·057
8–24	1·02 ± 0·015	1·05 ± 0·018	1·07 ± 0·010	1·01 ± 0·025

General mean 1·033 ± 0·007.
Standard deviation for single observation 0·075 ± 0·005.

Three general conclusions can be drawn. (1) The value of the Schwarzschild constant is independent of the duration of the exposure up to 24 hr. (2) The value of this constant is independent of the density of the print, except in the case of the exposures of medium duration, where there is a definite fall at high densities. It should be pointed out that in the limit, of course, the Schwarzschild constant must fall to 0 as the density increases, since there is a definite limit to the density which can be produced by any amount of illumination. The densities used were all well below this limit. (3) The departure from the reciprocity law is barely significant. In addition, it was shown that the value of the Schwarzschild constant is unaffected by changes, over wide limits, in the duration of fixation, or in the concentration or temperature of the hypo used. A few not very accurate measurements were made on unfixed prints; in these, the value of the constant was about 1·5.

The value of the standard deviation indicates an uncertainty of ±7·5% for a single measurement. This includes the uncertainty in the constancy of the illumination in two experiments, as well as the uncertainty in the matching of the densities, and the lack of uniformity of the emulsion, but does not include the uncertainty in the value of the wedge constant. The effect of this will become proportionately greater as the total illumination measured becomes greater. It may be expected, therefore, that the uncertainty in the determination of an unknown illumination will be between ±5 and ±10%.

B. *Gaslight paper* (*Illingworth Slogas matt soft*). A smaller number of determinations was made with gaslight paper, as it very soon became apparent that this emulsion is not suited for photometric work involving long durations of exposure. The value of the Schwarzschild constant as shown in Table IV is considerably less than 1 and appears to fall with increase in the duration of the exposure.

TABLE IV. THE SCHWARZSCHILD CONSTANT FOR GASLIGHT PAPER. (MEAN OF ALL PRINT DENSITIES)

Duration of exposure, hr.			
3/4	3/4–3	3–15	15–30
0·94 ± 0·01	0·88 ± 0·02	0·80 ± 0·02	0·81 ± 0·03

Jones & Huse (1923) give values of the Schwarzschild constant for three types of emulsion; at very low intensities (exposures lasting up to a few hours) they find values of 0·63 for a high speed emulsion, 0·88 for a medium speed emulsion, and 0·68 for a low-speed emulsion. In all cases the value of p fell as the intensity of illumination was reduced. Baker (1924), working on three brands of panchromatic emulsion and with exposure times up to 200 sec., reports values of 0·80–0·93. Again, the value fell as the exposure time was increased.

The Spectral Sensitivity of the Emulsions. In all photometric methods it is important to know at least approximately the limits of wave-length to which the method is sensitive. For biological work, moreover, it is desirable that these limits should at least be within the visible spectrum. Spectral sensitivity curves of various photographic emulsions to tungsten filament light are given by Davis & Walters (1922). These authors find that ordinary plates have a maximum sensitivity to light of wave-length between 450 and 475 mμ., while the slower transparency and lantern plates have a maximum sensitivity in the region 420–460 mμ. These curves, however, give little indication as to the spectral sensitivity to be expected from an emulsion such as P.O.P. which is not developed.

Accordingly, fresh observations were made with a Hilger quartz spectrograph, using an automobile head-lamp bulb as source of light; under the conditions of operation, the colour temperature would have been about 2800° K.; a slit width of 2 mm. had to be used to get a sufficiently high illumination to affect P.O.P. in a reasonable time. The approximate sensitivity curves shown in Fig. 2 were obtained by making a series of exposures of different durations and plotting the wave-length at which a standard amount of blackening had been produced, against $1/t^p$, where p is the Schwarzschild constant for the emulsion in use. Each ordinate was then corrected for the varying dispersion of the spectrograph and the varying obliquity of the light falling on the paper.

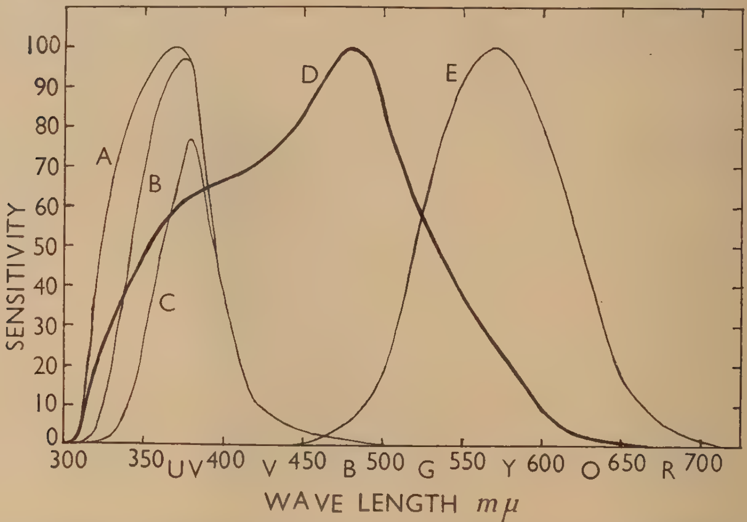


Fig. 2. Spectral sensitivity curves to tungsten filament light. *Ordinates*: Sensitivity in arbitrary units. *Abscissae*: Wave-length. (A) Illingworth Slogas. (B) The same with neutral tint wedge (zero end) in front of slit, i.e. showing the effect of absorption by the glass mounts. (C) The same with neutral tint wedge (density = 1·0) in front of slit, the ordinates being multiplied by 10. (D) Ilford P.O.P. (E) The human eye. Curve *E* is derived from the luminosity figures of Gibson & Tyndall (1923) and the distribution of energy with wave-length in tungsten filament light given by Priest (1922).

The curve for gaslight paper differs very markedly from that given by Davis & Walters for ordinary photographic plates, the maximum sensitivity being in the neighbourhood of 370 mμ. As a check, a series of exposures was made on an Imperial S.R. plate; the maximum sensitivity was found to be around 465 mμ., in good agreement with the observation of Davis & Walters. The shift of the maximum sensitivity towards the shorter wave-lengths in the case of gaslight paper is in agreement with the similar but smaller shift observed by Davis & Walters in the case of transparency and lantern slide plates.

The behaviour of P.O.P. is very different. If the unfixed print is examined (Fig. 3) it will be seen that the blackening begins at a wave-length of about 370 mμ. The density, however, does not increase at all rapidly in this region, but extends toward the red end of the spectrum, the maximum density after 32 hr. exposure being produced at about 520 mμ. It is to be supposed that the surface layers of the emulsion become blackened first, and that these then absorb the shorter wave-lengths more than the longer, and so prevent the former from penetrating to the deeper layers. On fixing, the density of the whole print is reduced, and the weak effects of the short wave-lengths in the short exposures are removed entirely. The most effective wave-length for the fixed print, i.e. that at which blackening is first produced, is thus shifted to about 485 mμ. Introduction of the dispersion correction, shifts this maximum to 480 mμ.

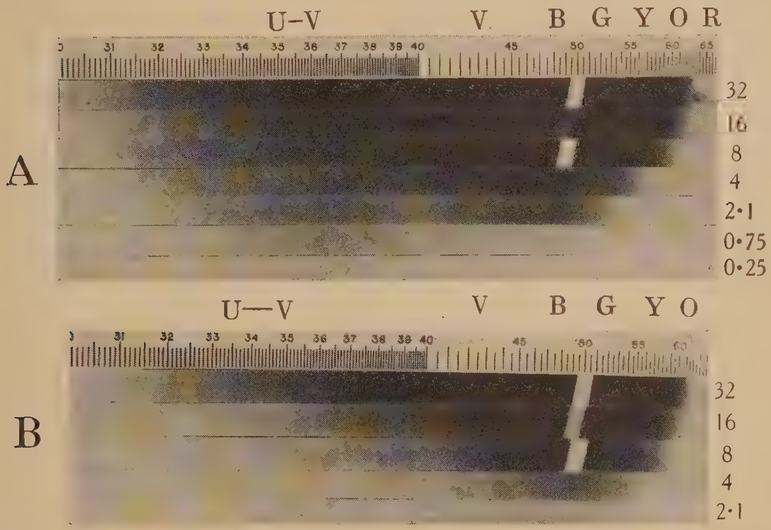


Fig. 3. Photographs of continuous spectrum of tungsten filament light taken on P.O.P. (A) Unfixed. (B) Fixed. The duration of each exposure is given in hours. The white mark across the upper three exposures in each case is due to the glass plate which was placed in front of the paper cracking during the 16 hr. exposure; this was made before the 8 hr. exposure.

It is clear, therefore, that for purposes of photometry in visible light, P.O.P. is greatly to be preferred to gaslight paper, or, in all probability, to any emulsion after development. Not only is it sensitive to a wider range of wave-lengths, but it has the added advantage of obeying the reciprocity law within the limits of experimental error.

STANDARDIZATION AND CALCULATION OF THE RESULTS

A 12 V., 36 W. automobile head-lamp bulb was used as standardizing light, operated from one of the current stabilizing circuits already described. An elaborate circuit of this kind is not necessary, as the exposure is only of a few hours' duration, and the current can easily be regulated by hand. The paper was exposed to this light at a distance of 30 cm., a sheet of flashed glass being placed in contact with the lamp bulb. Three exposures were usually made for about 2, 4 and 6 hr. respectively, giving three patches of different density. The wedge print was then compared with each of these patches in turn exactly as described above for the determination of the Schwarzschild constant. The mean of the three results was then taken. The method of calculation is indicated by the following example.

An exposure was made on the roof of the Plymouth laboratory from 20.30 G.M.T. 12 July 1934 to 20.30 13 July, say 17 hr. of daylight. The weather was mainly overcast. No diffusing screen was used and consequently the exact value of the wedge constant to be used is a little uncertain. The results are given in Table V, in terms of the intensity of the standardizing light. If this is measured in visual units, then the unknown illumination can also be directly expressed in visual units, provided that the distribution of energy with wave-length is the same in the unknown as in the standardizing source of light. For other sources of light—notably daylight—correction factors are necessary. The magnitude of these colour correction factors are subject to very considerable uncertainty since the methods used in their derivation fail to take more than an approximate account of the behaviour of photographic emulsions in lights of different intensities and different wave-lengths. Measurements made in any one quality of light, however, will be consistent among themselves even though their absolute magnitudes in visual or energy units are uncertain. The object of the standardizing exposure is primarily to eliminate random differences between one sheet of paper and another, arising from inherent differences of sensitivity, or from small differences in processing.

TABLE V. ANALYSIS OF A TYPICAL RECORD

Recorder on roof of Laboratory 20.30 12 July to 20.30 13 July

Duration of standardizing exposure, hr. (t_s)	Mean distance along wedge print to point of density match, mm. (l)	D ($=kl$) ($k=$wedge constant)	Log R/I_s ($=D+\log t_s$)	R/I_s corrected for $p=1·03$
1·9	104	3·15	3·43	2580
3·0	86	2·90	3·37	2240
5·0	72	2·71	3·41	2480
				Mean 2435

These correction factors express the relative brightness of the two sources of light as measured by (1) the human eye, and (2) the photographic emulsion. The relative brightness to the human eye on the one hand, and to the photographic emulsion on the other hand, of tungsten filament light can be discovered from a knowledge of (*a*) the luminosity curve of a constant energy spectrum (Gibson & Tyndall, 1923), (*b*) the distribution of energy with wave-length in the tungsten filament light (Priest, 1922), and (*c*) the spectral sensitivity curve of the photographic emulsion to tungsten filament light, described in the previous section. The ratio between the area below the luminosity curve for tungsten filament light and that below the photographic spectral sensitivity curve for the same light, gives us the photographic effectiveness of each lux of this light; we will denote this by E_w. For daylight, a similar factor can be derived from (*a*) the luminosity curve as above, (*b*) the distribution of energy with wave-length in daylight (Davis & Gibson, 1931), and (*c*) the spectral sensitivity curve of the photographic emulsion to daylight, derived from the similar curve for tungsten filament light by means of the two energy distribution curves; we will denote this factor by E_d.

The figures used for daylight are those given by Davis & Gibson for the distribution of energy with wave-length in the sun's radiation outside the earth's atmosphere. These authors give reasons for believing that the colour temperature of an overcast sky is very closely equal to that of the sun outside the earth's atmosphere.

The figures given by Priest (1922) for the energy distribution with wave-length of a tungsten filament lamp, are for a lamp with an efficiency of 15·6 lumens per watt. The distribution of radiant energy in the plane of the filament used under normal operating conditions (11·6 V., 2·8 amp.) was measured approximately by means of a photo-cell, and the luminous efficiency calculated to be about 16 lumens per watt, a sufficiently close approximation for the present purposes.

The illumination on the photographic paper when exposed to the standardizing light was measured by means of a Holophane Lumeter, and found to be 550 lux. The value of E_w was found to be 0·26, so that the "photographic" intensity of the standardizing light was $550 \times 0{\cdot}26 = 143$ "photographic units". Similarly, the value of E_d was found to be 0·69, so that if we have a daylight illumination which is, photographically, A times the standard of 143 photographic units, its visual intensity will be $\frac{143 \times A}{0{\cdot}69}$. Thus in the example given in Table V, the total vertical illumination received becomes $2435 \times \frac{143}{0{\cdot}69} = 505$ kilolux-hours. The recorder, in this experiment was placed on a horizontal surface, and so the readings represent the vertical component only of the total illumination. There is no reason why a photographic recorder of this type should not be placed within a globe integrator, such as is described by Atkins & Poole (1936*a*), in which case the total illumination from all directions would be measured.

The question now arises as to the appropriate value to be used for the factor E_d during bright sunshine. Owing to the scattering in the upper atmosphere, sunlight at the earth's surface is relatively deficient in the blue end of the spectrum, the scattered light being apparent in the blueness of the clear sky. If the recorder is placed in a spherical integrator, so that it receives the whole radiation from the celestial hemisphere, the direct sunlight and the scattered skylight would be recombined, and the value 0·69 would still be appropriate for the factor E_d. When used to record the vertical component only, it will receive one-half of the scattered skylight, and a fraction of the direct sunlight depending on the altitude of the sun. From the figures given by Davis & Gibson (1931), it can be calculated that the photographic effectiveness (P.O.P.) of each lux of mean noon sunlight is 0·46, and the calculated values of E_d for various altitudes of the sun are given in Table VI. The low value for very low altitudes is only estimated; when the sun is very low, there will be a considerable amount of scattering by the thick layer of atmosphere, and the sunlight will be distinctly yellow. Moreover, this yellow light will be reflected by the under surfaces of clouds and mist, and so will not be compensated by the blueness of the sky. In view of the very great variability of light conditions at sunrise and sunset, it would be unwise to place any reliance on photographic observations made at these times.

TABLE VI. THE PHOTOGRAPHIC EFFECTIVENESS OF DAYLIGHT + SUNLIGHT FOR P.O.P.

Altitude of sun	75°	50°	38°	30°	10° and less
Value of E_d	0·62	0·64	0·665	0·69	0·60 and less*

* According to amount of mist and cloud.

It should, perhaps, be pointed out, to avoid misconceptions, that we are not concerned, here, with the relative intensity of the sunlight and the skylight. As is shown by the figures given by Atkins & Poole (1936*b*), this quantity varies very greatly according to the altitude of the sun, the time of year and type of sky. We are concerned only with the apparent colour temperature of the light falling on the photographic recorder. Two extreme examples will illustrate the difference between these two quantities. (1) Outside the earth's atmosphere, there is no skylight (to all intents and purposes), and the intensity ratio sun/sky is infinity. (3) When the sky is completely overcast, there is no sunlight, and the intensity ratio is zero. Yet the colour temperature in both cases is the same.

USE OF THE METHOD IN THE FIELD

The detailed technique must depend upon the exact nature of the measurements to be made, and the only essentials are some means of clamping the wedge in contact with the sensitive paper, and suitable protection from the weather. That part of the paper which is not underneath the wedge must be protected from the light, so that the standardizing exposure or exposures may be made on the same sheet. There is no necessity to perform the standardization in the field. The prints, if reasonably cool and dry, can be kept in the dark without deterioration certainly for a week, and probably for longer, before fixing. When used on land, and in bright sunlight, the recorder should be placed as far as possible so that the direction of the sun is at right angles to the long axis of the wedge; the small errors due to the parallax between the wedge and the emulsion are thus eliminated.

SUMMARY

1. The photographic neutral-tint wedge method of measuring the total illumination falling on an area over a long period of time is described.

2. A study is made of the chief sources of error inherent in photographic methods, i.e. (*a*) the uncertainty in the value of the wedge constant, and (*b*) the failure of the reciprocity law, in that the amount of blackening of the photographic emulsion is not, in general, strictly proportional to the product of the intensity of the illumination and the duration of the exposure.

3. It is shown that P.O.P. obeys the reciprocity law sufficiently closely for durations of exposure between 1 and 24 hr. Gaslight paper, on the other hand, can only be used when the duration of exposure is less than about 1 hr.

4. It is shown that when P.O.P. is used, and a sheet of diffusing glass is placed above the wedge, the value of the wedge constant is sensibly independent of the direction and quality of the incident light.

5. Spectral sensitivity curves to tungsten filament light for gaslight paper and P.O.P. have been evaluated. From these, and other data, correction factors have been calculated for converting the photographic measurements of illumination into visual units.

6. It is concluded that the method is sufficiently reliable for use in the field, where its simplicity and the small amount of apparatus required, make it specially suitable. The experimental uncertainty is about ±5 to ±10%.

REFERENCES

Atkins, W. R. G. & Poole, H. H., 1936*a*. The photo-electric measurement of diurnal and seasonal variations in daylight, and a globe integrating photometer. *Phil. Trans. Roy. Soc.* A, Vol. 235, p. 245.

—— —— 1936*b*. Photo-electric measurements of the luminous efficiency of daylight. *Proc. Roy. Soc.* B, Vol. 121, p. 1.

Baker, E. A., 1924. The law of blackening of the photographic plate at low densities. *Proc. Roy. Soc. Edin.* Vol. XLV, p. 166.

Benson, D. E., Ferguson, W. B. & Renwick, F. F., 1918. A convenient and accurate photometer for the measurement of photographic densities. *Photogr. Journ.* Vol. 58, p. 155.

Cooper, J. O. & Sayce, L. A., 1932. A photographic daylight recorder. *Journ. Sci. Inst.* Vol. 9, p. 282.

Davis, R. & Gibson, K. S., 1931. Filters for the reproduction of sunlight and daylight and the determination of colour temperature. *Bur. Stand. U.S.A. Misc. Publ.* No. 114.

Davis, R. & Walters, F. M., 1922. Sensitometry of photographic emulsions and a survey of the characteristics of plates of American manufacture. *Bur. Stand. U.S.A. Sci. Papers*, Vol. 18, p. 1.

Dobson, G. M. B., Griffith, I. O. & Harrison, D. N., 1926. *Photographic Photometry.* Oxford, University Press.

Eder, J. M., 1919. Ein neues Graukeilphotometer. *Photogr. Korr.* Bd. 56, p. 244.

—— 1920*a*. Ein neues Graukeilphotometer. *Photogr. Korr.* Bd. 57, pp. 1, 41, 83, 304.

—— 1920*b*. *Ein neues Graukeilphotometer.* Halle, Wilhelm Knapp.

Gibson, K. S. & Tyndall, E. P. T., 1923. Visibility of radiant energy. *Bur. Stand. U.S.A. Sci. Papers*, Vol. 19, p. 131. (Quoted by Ives, H. E., *Int. Crit. Tables*, Vol. 5, p. 436.)

Goldberg, E., 1910. The preparation of prismatic wedges of neutral colour for photometric work. *Brit. Journ. Photogr.* Vol. 57, p. 648.

Gruber, M., 1924. Über ein Methode zur Messung des Lichtgefälles im Wasser mit Hilfe des Eder-Hechtschen Graukeils. *Intern. Rev. f. Hydrobiol.* Bd. 12, p. 17.

Hecht, W., 1918. Das Graukeilphotometer im Dienste der Pflanzenkultur. *S.-B. Akad. Wiss. Wien.* II*a*, Bd. 127, p. 2283.

Hull, A. W., 1929. Hot cathode thyratrons. *Gen. Elect. Rev.* Vol. 32, pp. 313, 390.

Jones, L. A. & Huse, E., 1923. On the relation between time and intensity in photographic exposure. *Journ. Opt. Soc. Amer.* Vol. 7, p. 1079.

Mallett, R. A., 1922. On the failure of the reciprocity law in photography. *Phil. Mag.* Vol. 44, p. 904.

—— 1923. On the failure of the reciprocity law in photography. *Phil. Mag.* Vol. 45, p. 800.

Oberdorfer, E., 1928. Ein neuer Apparat zur Lichtmessung unter Wasser. *Arch. f. Hydrobiol.* Bd. 20, p. 134.

Priest, I. G., 1922. Colour temperature of high-efficiency sources by the rotatory dispersion method. *Journ. Opt. Soc. Amer.* Vol. 6, p. 27. (Quoted by Coblentz, W. W., *Int. Crit. Tables*, Vol. 5, p. 245.)

Schwarzschild, K., 1900. On the deviations from the law of reciprocity for bromide of silver gelatine. *Astrophys. Journ.* Vol. 11, p. 89.

Toy, F. C. & Ghosh, J. C., 1920. The absorption of light by the Goldberg wedge. *Phil. Mag.* Vol. 40, p. 775.

NOTES ON THE BREEDING OF SOME LAMELLIBRANCHS FROM PLYMOUTH AND THEIR LARVAE

By Marie V. Lebour, D.Sc.
Naturalist at the Plymouth Laboratory

(Text-figs. 1–7)

CONTENTS

	PAGE
Introduction	119
Notes on the breeding seasons of certain lamellibranchs	123
The larvae and post-larvae of:	
Ensis and *Cultellus*	126
Some species of *Cardium*	129
Pholadidea loscombiana and *Barnea parva*	132
Teredo at Plymouth	135
The larvae of *Hiatella arctica* and *H. gallicana*	138
The larva and post-larva of *Heteranomia squamula*	140
The larvae and post-larvae of *Mysella bidentata* and a closely related species	142
References	144

INTRODUCTION

A study of the larval stages of different lamellibranchs from Plymouth with a view to determining their importance in the plankton has brought out some interesting facts. It is well known that the free-swimming larvae are much simpler than most of the gastropod veligers, and that the velum is usually entire, having rarely a slight indentation, showing a tendency to be bilobed in the larger forms. They thus resemble in this respect the primitive gastropods. In many of them the velum is lost early in life, and usually the change in form of the shell takes place after metamorphosis. The post-larval growth is therefore an important part of the life history. The first shelled stage is so similar in all species that it is almost impossible to distinguish the different early veligers in the plankton, but in certain cases fertilizations have been made and the larvae reared until they have lost the velum and descend to the bottom when the species, or at least the genus, can usually be identified.

Fertilizations were found to be difficult. Those which were successful were made in finger-bowls in the usual way, in sterilized or filtered water, the free-swimming larvae being transferred to plunger jars or small bowls with minute flagellates for food. Veligers from the plankton were kept in bowls or plunger jars with flagellates or diatoms for food until they grew to a stage in which the species or genus was recognizable. In this way much useful knowledge has been gained. Adults of many species were examined to find the state of the gonads and the breeding seasons. This, together with the recognition of the larvae in the plankton, has shown many definite breeding periods, and certain veligers at times dominate the plankton, such as *Mytilus edulis* in late spring and early summer and *Ensis siliqua* in early spring.

Descriptions of the larvae and post-larvae of *Lima hians* and of *Kellia suborbicularis* have already been published (Lebour, 1937–1938). Notes on several other species are given below; though unfinished it is thought best to publish them now, since the work must be discontinued for a period owing to my absence from Plymouth.

Knowledge of the later lamellibranch larvae and post-larvae is slight except for those which are economically important. References to these latter are purposely omitted in the list of literature, and only a selection of the more important papers relating to lamellibranch larvae is here included. The bulk of the previous work has been done on the egg and newly hatched larva. We have, however, the researches of Drew (1901) on *Nucula* and *Yoldia*, Odhner (1914) on various larvae from Rovigno, Pelseneer (1926) on *Lucina*, and Kändler (1926), who reared several planktonic veligers to recognizable forms, his work being quoted extensively by Haas in Bronn's *Tierreich* (1929, 1937). Thorson (1935) described the eggs and young of *Musculus*, and Matthews (1913) reared *Mytilus edulis* from fertilization to the young sessile stages. All these papers deal with species which occur in Britain or with closely related forms. In Japan Miyazaki (1935, 1936) has reared several species from fertilizations to young sessile stages.

The descriptions show that most of the essential external changes take place after the velum is lost. This, however, does not by any means indicate that the free-swimming larvae are of no account in the plankton, for they are often present in very large numbers and are known to be eaten by many planktonic and other animals. They are found in very small herring before the loss of the yolk sac, and young sprat of whitebait size frequently have their stomachs full of early veligers (Lebour, 1921). The best food for rearing crab larvae was found to be the larvae of the common oyster taken from the gills of the parent, and *Teredo* larvae one day old, obtained from fertilizations, were also found useful for this purpose (Lebour, 1927). Many small invertebrates eat lamellibranch larvae; to quote but one instance, the larvae of the annelid *Magalona* is always found to be feeding on them (Lebour, 1922).

Most lamellibranch veligers are small, the largest being well under 0·5 mm. long. A striking fact shown in the present study is that some of the largest veligers belong to very small adults. Thus an unusually large larva is found in *Kellia suborbicularis*, reaching to 0·32 mm. in shell length, the outstretched velum being still larger (Lebour, 1938), and two only slightly smaller turn out to be closely related forms, *Mysella bidentata* and a species which is possibly undescribed (see below, p. 143). Both *Kellia* and *Mysella* are small when adult, *Kellia* breeding at a shell length of from 4 to 9 mm., while *Mysella* is still smaller. Both are viviparous; the larvae are retained in the gill pouch until an early shelled stage, and the remainder of the larval life is continued for some time freely in the sea. All of these veligers are round or roundish.

Lima is a striking member of the plankton in its larval stage (Lebour, 1937) at certain times of the year; it often occurs with *Kellia*, and is easily recognizable by its triangular wedge-shaped shell attaining a large size before losing the velum. *Hiatella arctica* also grows to a large size, the shell being triangular with its greatest diameter lengthways. *Kellia*, *Lima* and *Hiatella arctica* are the commonest large lamellibranch larvae at Plymouth. Of these *Kellia* may occur throughout the year, the others chiefly in late summer and autumn. *Hiatella gallicana* breeds in winter and its larva, smaller than that of *H. arctica*, occurs in winter and early spring. *Heteranomia squamula* is also easily recognizable in the plankton on account of its very conspicuous pedal sinus (see below, p. 140), *Anomia* being similar but without such a distinct sinus. Both occur irregularly throughout the year, *Heteranomia* especially in autumn and winter. *Ensis siliqua* characterizes the plankton in early spring, apparently its only breeding season; the larva can be recognized by its oval shell curving in dorsally behind and by its bright yellowish brown liver. The closely related larva of *Cultellus pellucidus* occurs in autumn and winter and is distinguishable from *Ensis* by the red colour near the siphons in the late larva (see below, p. 128). *Mytilus edulis* is by far the commonest larva in May and June, occurring also sparingly at other times; it is recognizable by its conspicuous eye and purplish tinge. *Pecten* larvae and their near relatives also have conspicuous eyes, but the shell is more oval and not tinged with purple; moreover, early post-larvae are often seen with the beginning of the shell sculpture peculiar to these forms. Closely related to *Mytilus* is the larva of *Musculus*. This is larger than *Mytilus*, coloured dark brown and purplish and with the shell rounder.

Cardium larvae are small and inconspicuous except those of *Cardium crassum*, which grow to a large size and are conspicuous members of the plankton in the summer months (see below, p. 132). Another easily recognizable veliger is *Teredo*, almost certainly *T. norvegica*, which is almost spherical and very globose, occurring at almost any time of year, sometimes in numbers. A second *Teredo* veliger, found inside the parent and swimming about round the wood in which it burrows, is probably closely related to *T. navalis* (see below, p. 136). *Pholadidea* and *Barnea* lose the velum at a very early stage and are difficult to recognize in the plankton (see below, p. 132). *Venus fasciata* has a small round veliger, and probably the other members of the genus have similarly shaped larvae difficult to distinguish. Among the numerous small roundish and oval veligers that of *Abra* sp. (probably *Abra alba*) can be recognized and a few others guessed at, but there are still very many not identified. *Nucula nucleus* and *N. nitida* have free-swimming larvae; the egg of *N. nucleus* has been reared from a fertilization to a barrel-shaped larva similar to that described by Drew for *N. proxima*. It has been shown by Drew

(1901) that there is no typical velum in the family, but that the velar cells enwrap the larva in a case. The free-swimming stage is apparently very short in these two British species, for perfectly formed shells similar to the adults occur at a very small size.

It is found that a large number of different species of lamellibranch veligers occur in late summer and autumn, apparently after the second large diatom outburst. Although there are always some larvae present in the plankton more species occur at this season. The winter months have the fewest species; in spring and summer they are plentiful, but the plankton is frequently characterized by one predominating species.

A few lamellibranchs retain the larvae in the gill pouch until they have the adult form. This occurs in *Lasaea rubra*. Certain species of *Musculus*, as is shown by Thorson (1935), deposit their eggs in gelatinous strings, the young emerging as miniature adults. Several species are viviparous, notably the Erycinidae and their near relatives.

A table is given showing the fertilizations which have been successful. All those which resulted in egg division are marked. *Cardium edule*, *Cardium scabrum* and *Pholadidea loscombiana* were reared until they lost the velum and descended to the bottom. *Ensis siliqua*, *Barnea parva*, *Teredo norvegica*, *Hiatella gallicana*, *Spisula solida* and *Heteranomia squamula* were reared to the shelled larva, *Nucula nucleus* to the free-swimming larval stage.

TABLE I. SUCCESSFUL FERTILIZATIONS

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Nucula nucleus	.	.	.	.	.	.	×	.	×	×	×	.
Nucula turgida	.	×	.	.	.	.	.	.	.	.	.	.
Heteranomia squamula	.	.	.	.	×	.	.	.	.	.	.	.
Mytilus edulis	.	.	.	.	×	.	.	.	.	.	.	.
Chlamys opercularis	.	.	.	.	×	.	.	.	.	.	.	.
Cardium scabrum	.	.	.	.	.	.	×	.	.	.	.	.
Cardium edule	.	.	.	×	×	×	×	×	×	.	.	.
Venus ovata	.	.	.	.	.	.	×	×	×	×	.	.
Venus fasciata	.	×	.	×	×	.	×	.	.	×	×	.
Venus striatula	.	×	.	.	×	.	.	.	.	.	.	.
Paphia rhomboides	.	×	.	.	.	.	.	.	.	.	.	.
Paphia pullastra	.	.	.	.	.	×	×	.	×	×	.	.
Tellina crassa	.	.	.	.	.	.	.	.	.	.	×	.
Scrobicularia plana	.	.	.	.	.	×	.	×	.	.	.	.
Abra alba	.	.	.	.	×	.	.	×	×	×	.	.
Cultellus pellucidus	.	.	.	.	.	.	.	.	.	×	.	.
Ensis siliqua	.	.	×	×	.	.	.	.	.	.	.	.
Spisula solida	×	×	.	.	.	.	.	.	.	.	.	.
Aloidis gibba	.	.	.	×	.	.	.	.	.	.	.	.
Hiatella gallicana	×	×	.	×	×	.	.	.	.	.	.	.
Gastrochaena dubia	×	.	.	.	.	.	.	.	.	.	.	.
Barnea parva	.	.	.	.	.	.	.	.	×	.	.	.
Pholadidea loscombiana	.	.	.	.	.	.	.	.	×	×	×	.
Teredo norvegica	Any month											
Thracia convexa	.	.	.	.	.	.	.	.	×	.	.	.
Viviparous species extruding larvae:												
Kellia suborbicularis	.	.	.	.	.	.	.	.	×	×	.	.
Galeomma turtoni	.	.	.	.	.	.	.	.	×	.	.	.

The study of the post-larval stages has shown that two species exist of certain forms. Thus it is conclusively proved that *Hiatella gallicana* and *H. arctica* are distinct species, a fact often denied, but recognized by Winckworth (1932) and others. One breeds in winter, the other in spring, and the shelled veligers, as already shown by Odhner (1914), are easily distinguished. From the study of the post-larvae it is found that besides *Mysella bidentata* there is another very closely related species. The post-larval growth, that is to say the growth after the loss of the velum, is most interesting in many species, especially in the Pholadidae and Teredinidae. In *Pholadidea loscombiana* certain phases occur which are intermediate between the veliger and adult and peculiar formations are found in *Teredo*. The post-larval phases in *Pholadidea* seem to indicate a habit of life intermediate between swimming and boring which apparently lasts for a long time. The very young *Pholadidea* are never seen in the rock, and it may be that there is a prolonged period of crawling before any boring takes place.

NOTES ON THE BREEDING SEASONS OF CERTAIN LAMELLIBRANCHS

(The names are according to Winckworth, 1932)

Nucula nucleus (L.). Fertilized successfully in July, September, October and November. Reared to barrel-shaped larvae in July. No eggs or ripe sperm seen from December to March. Breeding from spring to early autumn. Eggs 0·10 mm.

Nucula hanleyi Winckworth. Breeding at the same time as *Nucula nucleus*.

Nucula turgida Leckenby & Marshall. Fertilized successfully in February and reared to free-swimming early larvae. Breeding in winter. Eggs 0·09 mm.

Glycimeris glycimeris (L.). Ripe eggs obtained in January, March and October; ripe sperm in January and March.

Arca lactea L. Ripe eggs in September and October; ripe sperm in January, June, September and October.

Anomia ephippium L. Ripe eggs in June and October. Larvae of this species or *Monia* are found in the plankton at any time of year.

Heteranomia squamula (L.). Successful fertilizations obtained in May and the larvae grew to an early shelled stage. Ripe eggs and sperm found at any time of year. Larvae are common in the plankton throughout the year but especially in autumn and winter when the breeding season is more intense.

Mytilus edulis L. Successful fertilizations obtained in May and the larvae grew to the young shelled stage. Mrs Matthews (1913) grew them successfully to young mussels. The chief breeding season is from April to June, but some may be found ripe at almost any time.

Modiolus modiolus (L.). Ripe eggs and sperm in December.

Musculus sp. (probably *M. marmoratus* (Forbes)). Veligers common in the plankton in late summer and autumn. Thorson (1935) found the eggs of *M. discors* and *M. niger* from East Greenland in strings close to the parent in Ascidians; they hatched out after the loss of velum. He states that *M. marmoratus* has small eggs hatching as veligers and it is therefore probable that the present species is *M. marmoratus*.

Chlamys varia (L.). Ripe eggs in July.

Chlamys distorta (da Costa). Ripe eggs and sperm in March and July.

Chlamys opercularis (L.). Eggs and sperm were given out in the laboratory tanks on May 25 1936. The eggs were successfully fertilized and grew to the young shelled stage. Post-larval stages are found throughout the year.

Chlamys tigerina (Müller). Ripe eggs and sperm in January. Larvae of *Chlamys* spp. not identified occur in any month of the year.

Lima hians (Gm.). Breeding from late summer to early spring. Larvae are most frequent in late summer and early autumn and are common in the plankton.

Astarte sulcata (da Costa). Ripe eggs were obtained in July and October, and ripe sperm in January and July.

Phacoides borealis (L.). Ripe eggs and sperm in March and April. Pelseneer (1926 as *Lucina lactea*) describes stalked egg capsules deposited on the sand.

Kellia suborbicularis (Montagu). Viviparous, giving out small shelled larvae from the gill pouch. Embryos found developing in the gill pouch in May, July and August; ripe sperm in May and October. The species apparently breeds throughout the year, as the larvae are present in the plankton in any month; but they are specially common in late summer and early autumn. Post-larvae have been found crawling on red rock and in rock crevices.

Galeomma turtoni Sowerby. Viviparous. Free-swimming embryos at an early stage without a shell were given out in September (obtained by Miss M. L. Popham).

Mysella bidentata (Montagu). Viviparous. Late veligers are common in the plankton in summer and autumn. Post-larvae and young are found in shell sand in autumn.

Mysella sp. Veligers common in the plankton in summer and autumn.

Cardium echinatum L. Nearly ripe eggs and ripe sperm found in January, April, May and September. Larvae have been taken in the plankton at various times.

Cardium scabrum Philippi. Fertilized eggs were obtained in July and were reared until the loss of the velum.

Cardium edule L. Breeding from spring to early autumn, chiefly May to August. Successful fertilizations were obtained from April to October and the larvae reared until the loss of the velum.

Cardium crassum Gm. Hermaphrodite. Apparently ripe eggs and ripe sperm found in almost any month. Larvae are taken in the plankton through spring and summer, and are often very plentiful.

Dosinia exoleta (L.). Apparently ripe eggs and ripe sperm in February and July.

Venus verrucosa L. Ripe eggs and sperm in April.

Venus ovata (Penn.). Breeding from March to October. Successful fertilizations were obtained in September and October and the larvae reared to an early free-swimming stage.

Venus casina L. Breeding throughout the year.

Venus fasciata (da Costa). Breeding throughout the year. Successful fertilizations were obtained in July and November, and the larvae reared to an early free-swimming stage.

Venus striatula (da Costa). Breeding in February, March and May. Eggs were successfully fertilized in February and May and reared to an early free-swimming stage.

Paphia rhomboides (Penn.). Breeding in October, November, December, February and March.

Paphia pullastra (Montagu). The chief breeding season is in summer, but the species breeds also in autumn. Successful fertilizations were obtained in June and September, and the larvae reared to an early shelled stage.

Paphia decussata (Gm.). Ripe eggs and sperm were found in summer months and also in December.

Tellina tenuis da Costa. Ripe eggs and sperm in May.

Tellina crassa Penn. Usually breeding in summer, but ripe eggs and sperm were also found in January. Successful fertilizations were obtained in July and the larvae reared to an early free-swimming stage.

Macoma balthica (L.). Active sperm in July.

Scrobicularia plana (da Costa). Breeding in summer. Eggs were successfully fertilized in June and July, and the larvae reared to an early free-swimming stage.

Abra alba (S. Wood). Breeding in summer. Successful fertilizations were made in May, August and October, and the larvae reared to an early free-swimming stage.

Gari tellinella (Lam.). Breeding in summer.

Solecurtus chamasolen (da Costa). Breeding in summer.

Solecurtus scopula (Turton). Nearly ripe eggs and sperm in July.

Cultellus pellucidus (Penn.). Breeding in late summer and winter, especially in winter. Successful fertilizations were made in September, but the eggs were reared only to the gastrula. Larvae are found in the plankton in autumn and winter.

Ensis siliqua (L.). Breeding in early spring. Eggs successfully fertilized in March and April were reared to an early shelled stage. Larvae are taken in the plankton in early spring.

Spisula solida (L.). Breeding in winter and early spring. Successful fertilizations were obtained in January and February, and the larvae reared to an early shelled stage.

Spisula subtruncata (da Costa). Active sperm in November and January; nearly ripe eggs in November.

Mya truncata L. One hermaphrodite with nearly ripe eggs and active sperm in May.

Aloidis gibba (Olivi). Successful fertilizations in April were reared to the gastrula stage.

Hiatella gallicana (Lam.). Breeding chiefly in winter, but also in spring. Eggs successfully fertilized in January, February, April, May and December were reared to an early shelled stage. Larvae are taken in the plankton chiefly in winter. Post-larvae are found in winter, crawling on red rock, into which they bore.

Hiatella arctica (L.). Breeding in summer. Larvae are taken in the plankton throughout the summer and autumn. They are especially common in late summer and early autumn.

Gastrochaena dubia (Penn.). Successful fertilizations were made in January and the larvae reared to the gastrula.

Barnea parva (Penn.). Breeding in summer and early autumn. Successful fertilizations were made in October and the larvae reared to an early shelled stage. The post-larva was reared in a plunger-jar from planktonic veligers taken in May.

Pholadidea loscombiana Turton. Breeding in autumn. In December nearly all were found to be spent females or males, and later all males. Eggs fertilized in September, October and November were reared until the loss of the velum and the beginning of post-larval growth.

Teredo norvegica Spengler. Breeding throughout the year. Successful fertilizations can be made at any time and the eggs were reared to the early shelled larvae. Veligers, almost certainly belonging to this species, are taken in the plankton in any month, especially in autumn.

Teredo sp. Viviparous. Adults with late veliger larvae were found in spring, but probably occur at other times also.

Thracia phaseolina (Lam.). Four hermaphrodite specimens nearly ripe were taken in July.

Thracia convexa (W. Wood). One hermaphrodite. The eggs were fertilized successfully in September and reared to the gastrula.

The Larvae and Post-larvae of *Ensis* and *Cultellus*

We know little of the breeding and larval stages of the Solenidae. Kändler (1926) at Heligoland reared *Cultellus pellucidus* from a planktonic veliger, with the shell 0·37 mm. long or less, to a young stage 1 mm. in length. The larval shell has a characteristic shape, narrowing at the anterior end, with a very conspicuous golden brown liver. The same shape, but with the anterior end slightly blunter, and a similarly coloured liver distinguish the larva of *Ensis siliqua* at Plymouth, which I have reared in a similar way until the characteristic teeth of *Ensis* were seen. This larva is very like that of *Cultellus* but differs in certain constant features noted below.

Ensis siliqua (L.) (Figs. 1 *a–g*)

This species is very common in sandy shores in the neighbourhood of Plymouth, especially at Millbay, Salcombe, and at Whitsand Bay. It was breeding freely in March and April, and in the early spring months the larvae characterized the plankton. Since these larvae rapidly disappeared towards early summer and the *Ensis* examined at other times of year were never ripe, it may be assumed that early spring is the usual breeding season here. Successful fertilizations were effected in March and April, the larvae growing to the shelled stage (Fig. 1 *a*) and then dying. Later larvae in the plankton were reared until the genus could be recognized.

Ensis siliqua is the only really common species (it is confused with *Ensis ensis* in the Plymouth Fauna List, 1931) and since the presence of the larvae in the plankton naturally followed the breeding of the species it may be safely assumed that the larvae are those of *E. siliqua*. Numbers taken at Millbay and Salcombe in March and April were ripe, and at other seasons no specimen examined was found to be breeding. Both ovaries and testes are cream-coloured and in the breeding season are very full of eggs and sperm. The eggs are small, 0·07 mm. in diameter, with a very thin membrane and no gelatinous covering. Shelled larvae were obtained in bowls from the fertilizations in two days. The shells were 0·10 mm. in length and slightly less in depth, the hinge being almost straight but slightly hollowed in the centre (Fig. 1 *a*). The velum was about half the length of the shell, and was surrounded by long cilia, but no large central cilium could be seen. These larvae did not live. Larvae of all sizes, from 0·16 to 0·35 mm. in length, abound in the spring plankton (Fig. 1 *b–d*), and some are seen even as early as February, dwindling at the end of April and almost absent in May and later. They resemble very closely the larvae of *Cultellus pellucidus* described by Kändler (1926), but the late larval stages and post-larvae do not have the characteristic orange-red pigment round the posterior mantle edge found in that species. Both have a very conspicuous golden brown liver, the shell being irregularly oval, narrowing

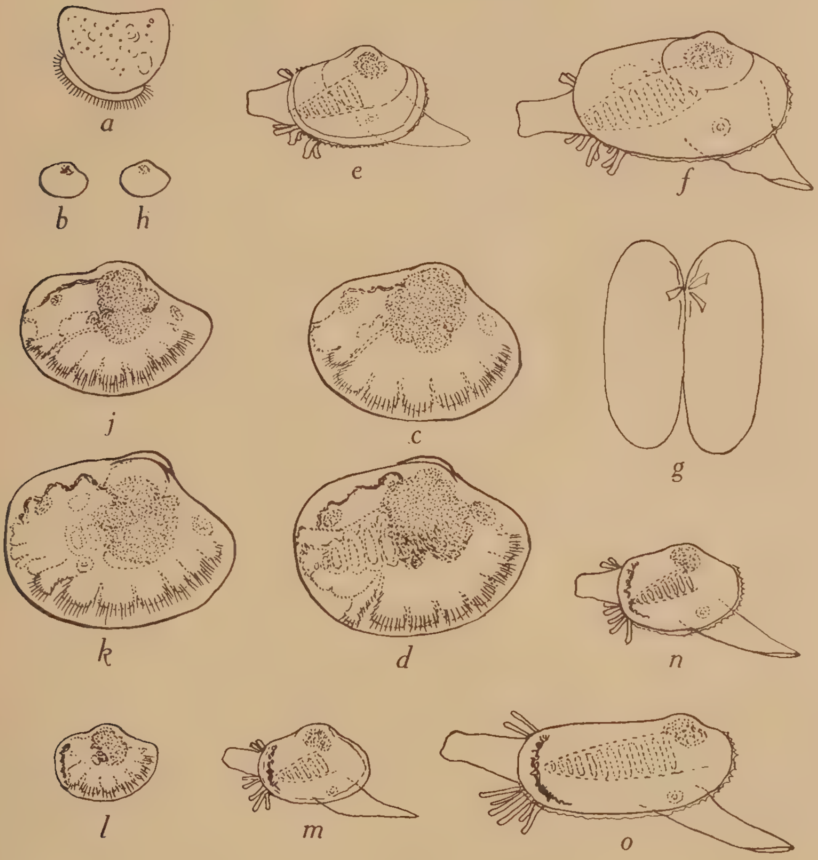


Fig. 1.

a–g, Ensis siliqua.

a, shelled larva from fertilization, 0·10 mm. long; *b*, smallest larva found in plankton, 0·16 mm. long; *c*, later larva from plankton, 0·28 mm. long; *d*, later larva just before losing velum, 0·35 mm. long; *e*, post-larva, grown in plunger-jar from planktonic veliger, 0·48 mm. long; *f*, post-larva, grown in plunger-jar from planktonic veliger, 0·72 mm. long; *g*, shell of post-larva, grown in plunger-jar from planktonic veliger, showing teeth, 0·72 mm. long.

h–o, Cultellus pellucidus.

h, smallest larva seen in plankton, 0·16 mm. long; *j*, later larva from plankton, 0·24 mm. long; *k*, later larva from plankton, nearly ready to metamorphose, 0·32 mm. long; *l*, later larva from plankton just before losing velum, 0·36 mm. long; *m*, post-larva grown in plunger-jar from planktonic veliger, 0·38 mm. long; *n*, post-larva grown in plunger-jar from planktonic veliger, 0·4 mm. long; *o*, post-larva grown in plunger-jar, 0·72 mm. long.

anteriorly, and rounded posteriorly, the umbo being prominent. The anterior end is sharper in *Cultellus* than in *Ensis*. In the larva of *Ensis siliqua* at 0·28 mm. long (Fig. 1 *c*) the velum is well developed and the animal is in much the same stage as Kändler's *Cultellus pellucidus* at 0·30 mm. At 0·35 mm. (Fig. 1 *d*), the largest larva seen, it is nearly ready to metamorphose but still retains a large velum. Five to seven gill slits may be present—a higher number than in Kändler's *Cultellus* at 0·36 mm. which has lost the velum—but the tentacles in the siphonal region have not yet appeared. There is, however, irregularity in the growth of the organs and in the size of the larva in both species at Plymouth.

These late larvae metamorphosed in a plunger-jar and became much elongated posteriorly, the original embryonic shell being still fairly conspicuous (Figs. 1 *e–g*). At 0·48 mm. the velum has completely disappeared, there are several gill slits and the siphons have developed with ciliated tentacles at their base, two above the dorsal siphon, which has a long extensile valve, and four below it, and two below the ventral siphon, as in *Cultellus* (Fig. 1 *e*). Later post-larvae were 0·72 mm. in length (Fig. 1 *f*, *g*) and showed the typical teeth of *Ensis* (Fig. 1 *g*), one cardinal in the right valve and two in the left, besides laterals. The foot is very large and powerful with a blunt flat tip and is capable of extensive jerky movements. Such older stages were in the plunger jars in January, having grown from the early spring veligers. It is probable, however, that they grew slowly and that in nature they would have attained this length much sooner.

Cultellus pellucidus (Pennant) (Figs. 1 *h–o*)

This species is often dredged in silty sand both inside and outside the breakwater, especially inside. It breeds in autumn and winter. Kändler found it breeding in Heligoland in November. Only one ripe female has so far been found at Plymouth at the same time as a male, and a partially successful fertilization was obtained at the end of September. All specimens examined in spring and summer were unripe except one male full of active sperm in July. The eggs from the fertilization only developed as far as a few segments.

Larvae attributable to this species and closely resembling those described by Kändler occur fairly commonly in the plankton in autumn and winter (November to January). The smallest seen was 0·16 mm. in length (Fig. 1 *h*), the largest 0·36 mm. (Fig. 1 *l*). They resemble very closely the larvae of *Ensis*, but the shell is more pointed anteriorly and the post-larvae are decidedly narrower in the shell. The orange-red pigment in the late larvae and post-larvae at the posterior end inside the mantle distinguishes them at once, as Kändler has already shown. Specimens grown in plunger-jars from the winter larvae in July measured 0·38 to 0·72 mm. (Figs. 1 *m–o*), the smallest being fully metamorphosed and agreeing well with Kändler's description.

THE LARVAE AND POST-LARVAE OF SOME SPECIES OF *CARDIUM*

It has been possible to differentiate between several *Cardium* larvae at Plymouth and to follow the growth of *Cardium edule* and *Cardium scabrum* from the egg to metamorphosis and post-larva.

The larva of *Cardium crassum* (*Laevicardium*) is easily recognized in the plankton and also another species which is almost certainly *C. echinatum*. *Cardium edule* and *C. scabrum* were reared from the fertilized egg to the time of metamorphosis and loss of velum. *Cardium crassum*, which is hermaphrodite, was not fertilized as up to the present it has not been possible to obtain really ripe eggs; but the larva, which is at times common in the plankton, was reared to a stage in which the species was recognizable. The veliger is much larger than that of either *Cardium edule* or *C. scabrum*, and the shell is smooth in the post-larva, even in those up to more than 1 mm. in length. *Cardium echinatum* was never obtained in a sufficiently ripe condition for successful fertilization, but the larva almost certainly attributable to this species is very unlike the others.

Cardium edule L. (Figs. 2 *a–j*)

Little is known of the late larval and post-larval stages of this species; it loses its velum very early and the ribs only appear after metamorphosis. At Plymouth it breeds in the late spring and summer months, although occasional exceptions may be found at other times. The veligers are chiefly found up the estuaries or in the sea near their openings in spring and summer. Successful fertilizations were made in April, May, June, July, August and September. The larvae were reared in bowls until the velum was lost, but they did not live to put on any ribs. Early and late veligers from the plankton corresponded with those reared, and post-larvae showing the same-sized embryonic shells were found in tow-nettings taken near the bottom in the estuaries. Later young stages were found in the estuaries. At Neal Point, in the Tamar Estuary, early in July, they were about 1 mm. in length, showing that spawning must have taken place some time before.

The eggs (Figs. 2 *a*, *b*) are covered with a thin membrane and a large gelatinous envelope in which development takes place until the veliger emerges. The unfertilized egg is 0·05 mm. across and is opaque with a large nucleus. It is surrounded by the closely fitting membrane which soon disappears, the large gelatinous covering being 0·16–0·18 mm. in diameter. The free-swimming veliger 3 days after fertilization measured 0·14 mm. in length; the hinge line of the shell was straight, the valves roundish and flat. The velum, armed with powerful cilia round the margin and a large central flagellum, was about half the length of the shell (Figs. 2 *c*, *d*). The internal organs were forming. In three weeks the shell was 0·16 mm. long (Fig. 2 *e*), the growth probably being slower than in natural conditions, and in five weeks it had increased to 0·30 mm. in length, the shell being nearly round and still perfectly smooth (Fig. 2 *f*). It now lost the velum and descended to the bottom. Although living for some time after this the reared larvae ceased to grow and eventually died.

Veligers of all sizes in the inshore plankton were similar to the reared specimen and none were larger than the largest reared. These, grown in plunger-jars and bowls, put on ribbed growth, the ribs at first being always very irregular. A growth of 0·05 mm. in three days was noticed in one. In all these post-larvae the embryonic shell can be recognized. Specimens 1 mm. in length from mud from the estuary show ribs more like the adult, but unarmed, and long tentacles in connexion with the siphons. The embryonic shell is still conspicuous (Figs. 2 *g–j*). Although so small the enormous numbers of these veligers must be very important in the plankton of the estuaries and inshore waters.

Cardium scabrum Philippi (Figs. 2 *k–q*)

This species is common in certain parts of the Sound and outside, especially on or in the crevice of the red rock dredged from Stoke Point grounds. Besides adults many post-larvae were found in this locality on the rock, often in small holes. Two adults were put together in a bowl and the next morning many eggs had been extruded. As these were all fertilized and beginning to segment, both a male and a female were probably present. The eggs lived and developed into larvae, some of which did well in bowls and reached the stage in which the velum was lost and the animal descended to the bottom. As with *Cardium edule* they grew no further, never putting on any ribs, and eventually they died.

Young *Cardium scabrum* are easily identified and many were reared from the planktonic veligers to a late post-larval stage in plunger-jars. The egg is similar to that of *C. edule* and almost the same size, the larva remaining in the gelatinous covering until it emerges as a free-swimming veliger (Fig. 2 *k*). The free-swimming shelled stage is at first very like that of *C. edule* but soon puts on concentric striations which are characteristic (Figs. 2 *l*, *m*). At 3 days old the shell is 0·08 mm. long, growing only to the small size of about 0·16 mm. long before losing the velum. The late larval shell is rather more oblong than in *C. edule*, and the concentric striae and small size at metamorphosis distinguish it. Post-larvae grown in plunger-jars from planktonic veligers put on irregular ribs, with the embryonic shell exactly similar to those reared from the egg showing very clearly (Figs. 2 *n*, *p*). The post-larvae are very much elongated posteriorly and nearly straight on the posterior dorsal margin which is highly spinous as are also the posterior ribs. Specimens about 1 mm. long are clearly distinguished from those of *Cardium edule* of the same size. At about 8 mm. the young shell is very like the adult and has become much rounder.

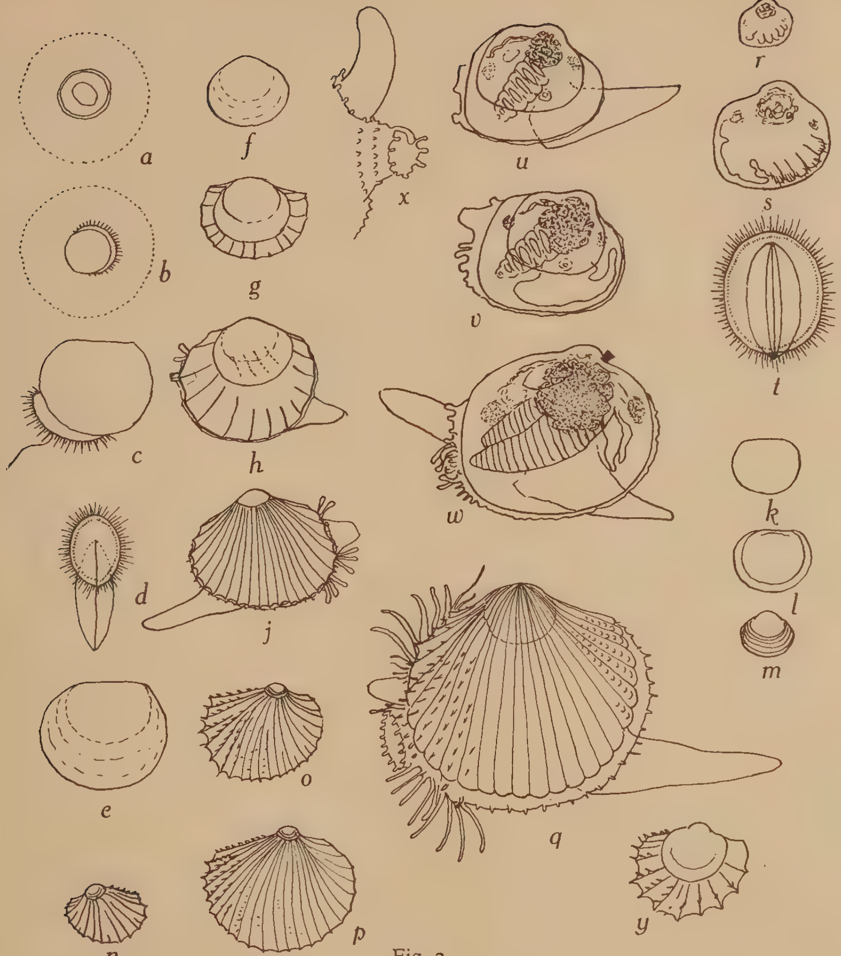


Fig. 2.

a–j, Cardium edule.

a, unfertilized egg, gelatinous covering, 0·18 mm. across; *b*, embryo in gelatinous covering, 24 hours old, from fertilization; *c*, free-swimming larva, 3 days old, reared from egg, shell 0·14 mm. long; *d*, the same swimming; *e*, older larva 0·16 mm., reared from egg; *f*, post-larva reared from egg, aged 5 weeks, 0·30 mm. long, having lost the velum; *g*, post-larva grown in bowl from planktonic veliger, 0·4 mm. long; *h*, later post-larva grown in plunger-jar from planktonic veliger, 0·48 mm. long; *j*, young *Cardium edule*, 1 mm. long from mud, Neal Point.

k–q, Cardium scabrum.

k, *l*, very young shells from fertilization, 0·07–0·08 mm. long; *m*, the same at loss of velum, 0·16 mm. long; *n*, post-larva grown in bowl from planktonic veliger, 0·56 mm. long; *o*, *p*, later post-larvae grown in plunger-jar from planktonic veliger, 0·8–1·12 mm. long; *q*, *Cardium scabrum*, 8 mm. long.

r–x, Cardium crassum.

r, smallest larva recognized from plankton, 0·2 mm. long; *s*, *t*, late veliger from plankton, ready to metamorphose, 0·44 mm. long; *u*, *v*, *w*, post-larvae reared from planktonic veligers in plunger-jars, 0·97–1·5 mm. long; *x*, siphons of a slightly older specimen.

y, post-larva of *Cardium echinatum* (?) reared from planktonic veliger in plunger-jar, 0·83 mm. long.

Cardium crassum Gmelin (Figs. 2 *r–x*)

Veligers of this species are common at times in the plankton in spring and summer, both inside and outside the breakwater. They are quite unlike those of *Cardium edule* and *C. scabrum*; they grow to a much greater size before losing the velum, and the shell is almost square posteriorly and in the post-larvae quite smooth in specimens up to at least a length of 2·5 mm. The smallest veliger recognized was 0·2 mm. in length (Fig. 2 *r*), and at metamorphosis and loss of velum it is about 0·4–0·45 mm. The velum is large and in the late stages overlaps the valves to a considerable extent (Figs. 2 *s*, *t*). Late larvae from the plankton reared in plunger-jars have the same square posterior end, the siphons gradually appearing with their tentacles, a very large and active foot, gill slits and conspicuous liver (Figs. 2 *u*, *v*, *w*). A specimen was reared in a plunger-jar to a shell length of 2·5 mm., showing the characters of this species.

Larva almost certainly attributable to *Cardium echinatum* L. (Fig. 2 *y*)

A veliger occurs at times in the plankton in spring, summer and autumn which almost certainly belongs to *Cardium echinatum*. The only other species it could be is *C. aculeatum*, and this is not nearly so common in the neighbourhood. Unlike the three larvae described above its valves are very much inflated, the shell with its two valves being almost globular. The veliger reaches a length of 0·48 mm. before metamorphosis. Specimens from the plankton reared in a plunger-jar put on growth with ribs and very sharp spines (Fig. 2 *y*).

Key to the larvae of the above species of *CARDIUM*

A. Larvae very small at metamorphosis, valves flat:
  (*a*) valves smooth (0·14–0·30 mm.) *C. edule*;
  (*b*) valves with concentric striations (0·07–0·16 mm.) *C. scabrum*.
B. Larvae large at metamorphosis:
  (*a*) valves fairly flat, square posteriorly (latest larva 0·44 mm.) *C. crassum*;
  (*b*) valves much inflated, round (latest larva 0·48 mm.) *C. echinatum* (?).

The Larvae and Post-larvae of *PHOLADIDEA LOSCOMBIANA* and *BARNEA PARVA*

All the free-swimming larvae known which belong to the Pholadidae have a more or less round shell and lose the velum at a small size. Kändler (1926) reared a species of *Pholas* (the species not identified but he thinks it is probably *Pholas dactylus* or *P. crispata*) from the planktonic veliger to a post-larva beginning to elongate. Miyazaki (1935) reared the Japanese species *Parapholas quadrizonata* up to a fairly late veliger from an artificial fertilization. In all these the embryonic shell (that is to say up to the period of metamorphosis) is round or nearly round, the elongation coming on later.

At Plymouth successful fertilizations were made of *Pholadidea loscombiana* and of *Barnea parva*. Unknown veligers from the plankton reared in plunger-jars developed into post-larvae almost certainly attributable to these two species, and in all of these the embryonic shell was small and nearly round. The veligers are so small and inconspicuous even in the late stages that it is very difficult to recognize them in the plankton, but when post-larval growth begins there are characteristics by which members of the family can be recognized. *Pholadidea loscombiana* was reared from the egg to the metamorphosis when it lost the velum, and to a post-larval stage in which it put on some anterior growth, but the post-larvae did not live longer. Post-larvae in the plunger-jars reared from veligers taken from the plankton almost certainly belong to this species, as well as a post-larva found on the surface of the red rock from Stoke Point grounds. As none of these grew to a sufficiently late stage the identification is, however, not certain. The fertilization of *Barnea parva* grew only as far as the early shelled stage. A post-larva found in a plunger-jar almost certainly belongs to this species and shows that it assumes the adult form at an extremely small size. Shell growth in the post-larvae of Kändler's *Pholas* and of both the forms mentioned above is put on anteriorly and posteriorly, the anterior growth beginning first in *Pholadidea*.

Pholadidea loscombiana Turton (Figs. 3 *a–o*)

This species is common round Plymouth, boring in rocks, especially in the red rock dredged at Stoke Point grounds. It breeds in autumn and winter, and in spring and summer is always unripe, or there are only males. Eggs were fertilized successfully in February, the end of September, October and November. Active sperm and apparently ripe eggs were seen in January and March, but fertilizations were not successful. Sperm only was seen from May to July. November is the month when all appear to be ripe and when the most successful fertilizations were made. The proportion of the sexes at this time is about equal. Fertilizations were made in bowls of filtered water, the active larvae a day old being transferred to a plunger-jar containing outside sea-water. Minute flagellates were given as food.

The unfertilized egg is pear-shaped and is 0·08 mm. in length (Fig. 3 *a*). When ripe the eggs are loose in the ovary. Both male and female gonads are cream-coloured and very large when ripe. When fertilized the egg contracted and became round, and was surrounded by a membrane (Fig. 3 *b*). With the membrane it measured 0·05 mm. It quickly lost the membrane and developed by the next day into a round larva, ciliated all over, with long hairs at one end. In two days there was a shell, 0·07 mm. long, with a straight hinge (Fig. 3 *c*). The velum was about half as long as the shell and circular in outline, but no central flagellum was seen. The shell became rounder and the velum larger (Figs. 3 *d*, *e*). Growth in the plunger-jar was very slow, the shell at four weeks old was only 0·24 mm. long, although the organs were well developed and three gill slits present. At this size the shell was pointed at the anterior end and rounded posteriorly. The foot was large and active, the velum nearly as long as the shell, and the larva ready to metamorphose. The larva then lost the velum and descended to the bottom, putting on anterior shell growth (Figs. 3 *f–k*). This growth was in the form of a smooth border on each valve turning outwards. No further growth took place and the larvae all died.

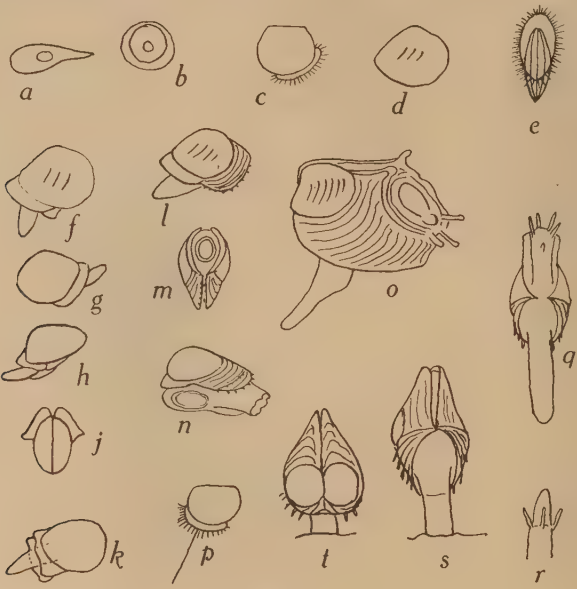


Fig. 3.

a–k, Pholadidea loscombiana.

a, unfertilized egg, 0·08 mm. long; *b*, fertilized egg, 0·05 mm. long; *c*, early shelled veliger, 0·07 mm. long, reared from egg; *d*, latest larva, 0·24 mm. long, reared from egg; *e*, the same swimming; *f–k*, post-larvae 0·24–0·26 mm. long, reared from egg.

l–o, probably *Pholadidea loscombiana.*

l, *m*, *n*, post-larvae from surface of red rock, 0·27–0·32 mm. long; *o*, post-larva reared from veliger in plunger-jar, 0·56 mm. long.

p–t, Barnea parva.

p, shelled larva 0·06 mm. long, reared from egg; *q*, *s*, *t*, young shell, 0·32 mm. long, reared from planktonic veliger in plunger-jar; *r*, extended siphon.

Post-larvae grown from unknown veligers in plunger-jars corresponded exactly with those reared from the egg, and having similar embryonic shells probably belong to this species (Fig. 3 *o*). The larvae reared from the egg were almost colourless until they lost the velum and then were yellowish with a purplish edge. The post-larvae from the plunger-jars were dark brown and purple and were possibly abnormal. A post-larval stage found on the surface of the red rock from Stoke Point grounds showed an anterior end very similar to that of the post-larva reared from fertilizations; it probably belongs to this species although it could not be kept alive long enough to be certain. It was 0·27 mm. in length. The embryonic shell was similar to that of *Pholadidea*; it had the form of one of the Pholadidae, small spines at the edge of the posterior elongated part, and a large siphon.

It is curious that no very young *Pholadidea* were found in the red rock, although careful search was made for them. It is possible that the post-larvae crawl about for a long time before settling down.

Barnea parva (Penn.) (Figs. 3 *p–t*)

Breeding of this species appears to be in summer and early autumn. It is common in the rocks at Rum Bay and, more rarely, with *Pholadidea* in the red rock of the Stoke Point grounds. A successful fertilization was obtained on September 15 1937, in a bowl of filtered water. The eggs are similar to *Pholadidea* but slightly smaller. The larvae lived only to the first shelled stages, 0·05–0·06 mm. across, and resembled *Pholadidea* but with a long central flagellum on the velum (Fig. 3 *p*). The later veligers were not recognized in the plankton, but a young stage grown from a mixture of planktonic veligers in a plunger-jar is almost certainly this species; it has the form of *Barnea* and young *Pholadidea*, but the embryonic shell is considerably smaller than it is in *Pholadidea*, being only 0·08 mm. in length and quite round. From the embryonic shell grow out two distinct portions, an anterior portion armed with spines and enclosing the foot, gaping very widely, and a posterior portion, the two parts of which can meet and enclose the siphon, but are also capable of gaping widely when the siphon is extended (Figs. 3 *q*, *r*, *s*, *t*). This specimen is only 0·32 mm. in its entire length, assuming the adult form very much earlier than does *Pholadidea*. The siphon is provided with tentacles surrounding a valve which is evertible.

The Larvae and Post-larvae of *Teredo* at Plymouth

Two species of *Teredo* occur boring in the raft near the breakwater, a small one closely related to *Teredo navalis*, but differing from it in certain important points, and *Teredo norvegica*. The first, like *Teredo navalis*, is viviparous. It keeps the veligers inside its body until they have attained a large size, the free veligers settling down on the wood and metamorphosing almost immediately they have left the parent. The second extrudes its eggs into the water before development takes place. Fertilizations were frequently made of *Teredo norvegica*, the larvae living until the young shelled stage. Late veligers, probably belonging to this species, occur fairly frequently in the plankton. In one instance one of these metamorphosed in a plunger-jar, and although not attached to wood grew to a post-larval stage in which the genus could be recognized. The larvae of the two forms are quite distinct and there is a great difference in the post-larvae.

Teredo norvegica Spengler (Figs. 4 *a–l*)

This species breeds throughout the year, judging from its eggs and sperm, which are ripe at any time. Fertilizations were frequently made during spring and summer when the larvae were used for feeding crab zoeae. The eggs are about 0·04 mm. across. The early shelled larva is about 0·05 mm. long with a straight hinge line and the velum is rather more than half the length of the shell (Figs. 4 *a*, *b*). Later larvae, probably this species, from the plankton, are nearly spherical with a velum nearly as large as the shell and a long foot with which they sometimes swim; the shell is 0·32 mm. long (Fig. 4 *c*). The latest larva is about 0·38 mm. long with a very large velum reaching far beyond the shell (Figs. 4 *d*, *e*, *f*). The sample of veligers from which the larvae metamorphosed possessed no eyes and came from inshore plankton in January. All through the autumn and winter they had occurred more frequently than at other times, although a few specimens may be seen in any month. The shell at metamorphosis is spherical and the one specimen which changed to a post-larva (Figs. 4 *j*, *k*, *l*) became slightly larger before the growth anteriorly of four hook-like spines on each valve, and in the centre of the ventral margin a long pointed outgrowth ending in a long spine which prevents the valves from shutting. The foot is very large and powerful and the siphons projecting at the posterior end are armed with stout tentacles. Five pairs of gill slits are present. This specimen, reared from a late veliger in a plunger-jar, was unfortunately lost.

In the plankton there are found at times veligers very like those described above but possessing eyes, some in the shape of a crescent and some large and round (Figs. 4 *g*, *h*). These also had the large foot which helped in swimming and were so similar in other ways that it seems probable that they belong to the same species and that some develop eyes and some do not.

Teredo sp. (Figs. 4 *m–p*)

This species differs from the description of *Teredo navalis* in its small size, the adults with young measuring under an inch in length, and in the shape of the pallets. It is hoped to investigate this further. Veligers of all sizes may be seen inside the body, the largest being about 0·32 mm. in length. The shell is, however, not quite spherical and slightly broader than long. This is not apparent when the animal is swimming, for it then appears to be round, the velum being about the same size as the shell (Fig. 4 *m*). The veligers emerge from the parent by means of the upper siphon and swim actively round the wood in which the parent bores. I have never seen them in the plankton. Larvae kept in plunger-jars and bowls metamorphosed into post-larvae, some on the wood. The post-larva at the loss of the velum is only slightly larger than the largest inside the parent. Almost directly the velum is lost there is formed a row of fine marginal spines anteriorly, followed quickly by a second (Figs. 4 *n*, *o*, *p*). The siphons with blunt tentacles begin to form, and ventrally there is a central pointed projection in the same position as in the post-larvae of (presumably) *T. norvegica*, but without a distinct spine. The blades inside the shell are long, reaching nearly half way down the shell.

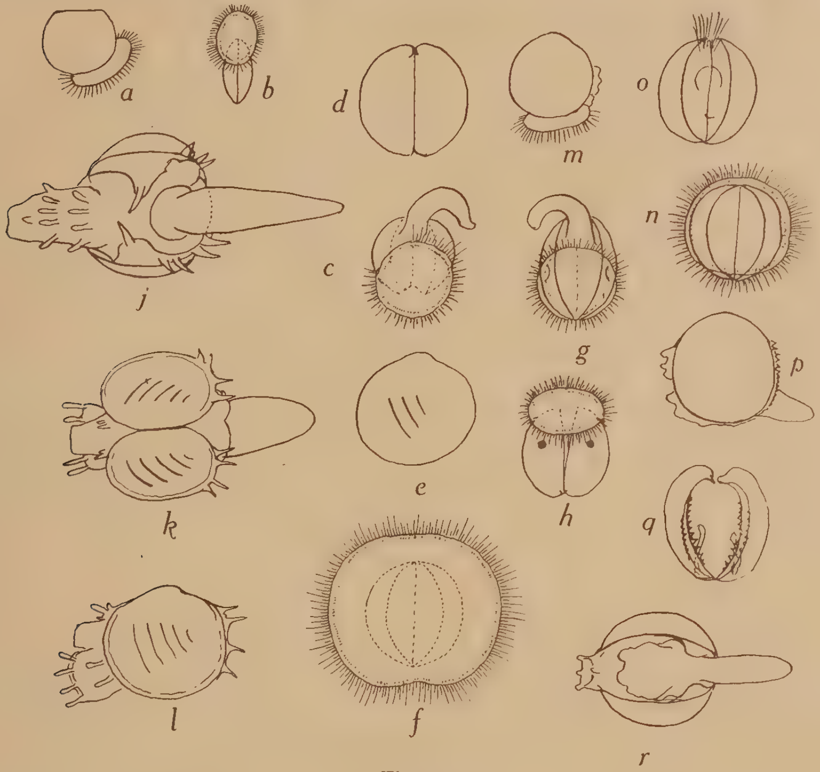


Fig. 4.

a–b, *Teredo norvegica*.

a, *b*, shelled larvae from fertilization, 0·05 mm. long.

c–l, almost certainly *Teredo norvegica*.

c–f, later veligers, 0·24–0·38 mm. long; *g*, *h*, veligers with eyes, probably this species; *j–l*, post-larvae reared from veliger in plunger-jar, shell 0·4 mm. long.

m–r, *Teredo* closely related to *Teredo navalis*.

m, young veliger, 0·24 mm. long; *n*, *o*, slightly older from parent, 0·32 mm. long; *p–r*, early post-larvae from wood.

The late larvae and post-larvae of this species are strikingly like those of *Xylotrya gouldi* described by Sigerfoos (1908), and are much more like them than those attributed to *Teredo norvegica*. Little has been done in the description of post-larval stages of Teredinidae and I have been unable to find in the literature any similar to those described above.

THE LARVAE OF *HIATELLA ARCTICA* AND *H. GALLICANA*

In the Plymouth Marine Fauna 1931, *Hiatella arctica* is listed as including *rugosa*. Winckworth (1932), however, again separates them. The larvae show that they are undoubtedly distinct species, as Odhner (1914) has already noted in specimens from Rovigno. Both species are common, *H. gallicana* (=*rugosa*) always or nearly always boring in stones, *H. arctica* usually free but occasionally found in holes in similar situations. *H. arctica* is not so common as *H. gallicana* and no fertilizations were made from it, but successful fertilizations were made from *H. gallicana*. They breed at different times: *H. gallicana* from autumn to early spring, *H. arctica* in summer. Larvae which developed into *H. gallicana* were present commonly in the plankton from autumn to spring, those of *H. arctica* being common in late summer and early autumn. The best locality for *H. gallicana* is in the red rock dredged from Stoke Point grounds, but the species is also found in the rocks at Rum Bay.

Hiatella arctica (L.) (Figs. 5 *k–q*)

The late larvae of this species are some of the commonest and largest veligers in the plankton, both inside and outside the breakwater at Plymouth, in summer and autumn, beginning about July and continuing to November or December. The late larva ready to metamorphose is about 0·36 mm. in length with a large velum about the length of the shell, the shell having concentric striae round the margin. It is usually a pinkish yellow, being redder towards the margin, but may be almost colourless. The liver is large and conspicuous, a dullish grey, and there are usually three gill slits present. The anterior end of the shell is more pointed than the posterior and the whole shell is somewhat triangular with the longest side ventrally (Figs. 5 *k*, *l*). At this size the velum is lost and layers of shell are formed all round, the anterior end being always more acute than the posterior, which is very square. At a length of 0·46 mm. there is one spine at the dorsal posterior end, the siphons have several blunt tentacles and there are five or six gill slits (Figs. 5 *m*, *n*). At a length of 0·56 mm. it has the same character, but there are two or more posterior dorsal spines (Fig. 5 *o*), whilst at 0·96 mm. there are two rows of large spines postero-dorsally (Fig. 5 *p*). A specimen reared in a plunger-jar grew to 1·44 mm. in length and had another row of spines dorsally (Fig. 5 *q*).

This late post-larva is very characteristic and grew many times from veligers in the plunger-jars. Similar specimens are to be found attached to weeds and hydroids in dredgings. The adults are often found in the neighbourhood of rocks.

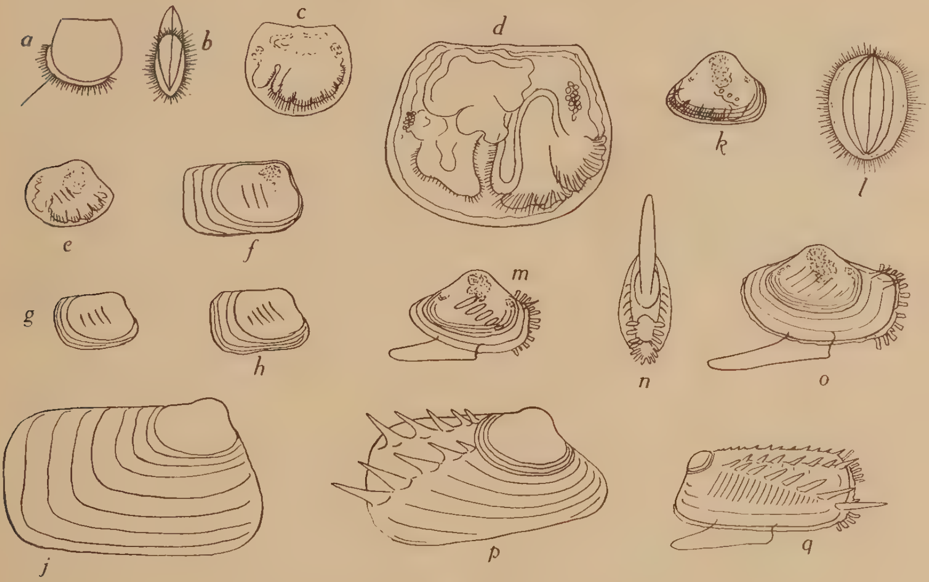


Fig. 5.

a–j, Hiatella gallicana.

a, *b*, shelled larvae reared from egg, 0·08 mm. long; *c*, *d*, the same, 0·12 mm. long; *e*, late larva from plankton, 0·32 mm. long; *f*, post-larva, 0·48 mm. long, grown from planktonic veliger in plunger-jar; *g*, *h*, post-larvae from red rock, 0·38–0·4 mm. long; *j*, young, 1 mm. long, reared from late veliger in plunger-jar.

k–q, Hiatella arctica.

k, *l*, late veliger from plankton, 0·36 mm. long; *m*, *n*, post-larvae grown from late planktonic veliger in plunger-jar, 0·46 mm. long; *o*, later post-larva grown from late planktonic veliger in plunger-jar, 0·56 mm. long; *p*, *q*, young reared from late planktonic veliger in plunger-jar, 0·96–1·44 mm. long.

Hiatella gallicana (Lam.) (Figs. 5 *a–j*)

Successful fertilizations of this species were obtained several times, particularly in winter and early spring. Late larvae from the plankton were reared in plunger-jars and bowls to the post-larval stages and young forms.

The eggs are pinkish although the ovary is usually a pinkish cream colour (Odhner (1914) states that the eggs of *Hiatella arctica* (= *Saxicava*) are red). The ripe egg is 0·05 mm. across, the free-swimming larva in less than 24 hours is about the same size, the shelled larva very soon after being about 0·08 mm. in length (Figs. 5 *a*, *b*) with the velum about two-thirds the length of the shell and provided with a large central flagellum. The shell has a straight hinge and the valves are slightly longer than broad.

In eight days the veliger was 0·12 mm. in length with the internal organs forming (Figs. 5 *c*, *d*). They did not grow after this and soon died. Late larvae from the plankton are roundish oval, more pointed anteriorly than posteriorly, 0·32 mm. in length (Fig. 5 *e*). At this size they lose the velum and put on anterior and posterior growth, especially posterior; usually they are without spines, but occasionally there are slight spines postero-dorsally in the same position as those of *H. arctica*. At a length of 0·48 mm. there are three gill slits in those grown in plunger-jars (Fig. 5 *f*). In some post-larvae found at the surface of the red rock in which the adult burrows there are four gill slits at a smaller size, the embryonic shell being smaller, and five at a length of 0·4 mm. (Figs. 5 *g*, *h*). Young stages reared from veligers in plunger-jars grew to 1 mm. and more, usually still without spines dorsally and of a squarish oblong shape, not so sharply pointed anteriorly as in *H. arctica* (Fig. 5 *j*).

The Larva and Post-larva of *HETERANOMIA SQUAMULA* (L.)

(Figs. 6 *a–f*)

This is the commonest species of the family Anomiidae at Plymouth. The adults abound on stones and other objects both inside and outside the breakwater, and the larvae are some of the commonest veligers in the plankton. Odhner (1914) has already described very similar larvae from Rovigno which he regards as *Anomia ephippium* and mentions another allied species.

Apparently the feature common to all anomiid larvae is the pedal sinus, which is very distinct in *Heteranomia*. This indentation is the beginning of the hole through which passes the byssus and eventually the plug for attachment. The lower (right) valve is flat, with the indentation; the upper (left) rounded, with a conspicuous umbo and a slight process ventrally which at first fits into the pedal sinus. Fertilizations were made in May and developed into shelled larvae, but the species may be ripe at any time. Specimens watched by Dr H. B. Moore in a situation in which he knew that the spat fall had occurred in February, were apparently ripe at a length of 5 and 6 mm. in March, active sperm being present and loose red eggs.

The early shelled larva (Fig. 6 *a*) was 0·05 mm. long with a slightly indented dorsal margin and the velum about two-thirds the length of the shell. No central flagellum was seen in the velum. The larvae from the fertilizations did not live, but the later veligers are very common in the plankton, both inside and outside the breakwater, at almost any time of year but especially in early autumn. The late larva nearly ready to metamorphose is about 0·18 mm. in length, the velum being large, slightly longer than the shell and the foot long and mobile. The larva swims actively shell downwards, the foot helping in the swimming (Figs. 6 *b*, *c*). The velum is soon lost, but specimens still retaining it with a shell length of 0·2 mm. may be seen (Fig. 6 *d*). The newly metamorphosed larva, from 0·2 to 0·23 mm. in length (Fig. 6 *e*) crawls on the bottom by means of a very long and contractile foot. At the umbo the early shell may still be seen. Specimens from the plankton which metamorphosed in plunger-jars grew to a large size and settled on the glass. At 0·45 mm. long the pedal sinus growing into the hole for the byssus is well shown (Fig. 6 *f*).

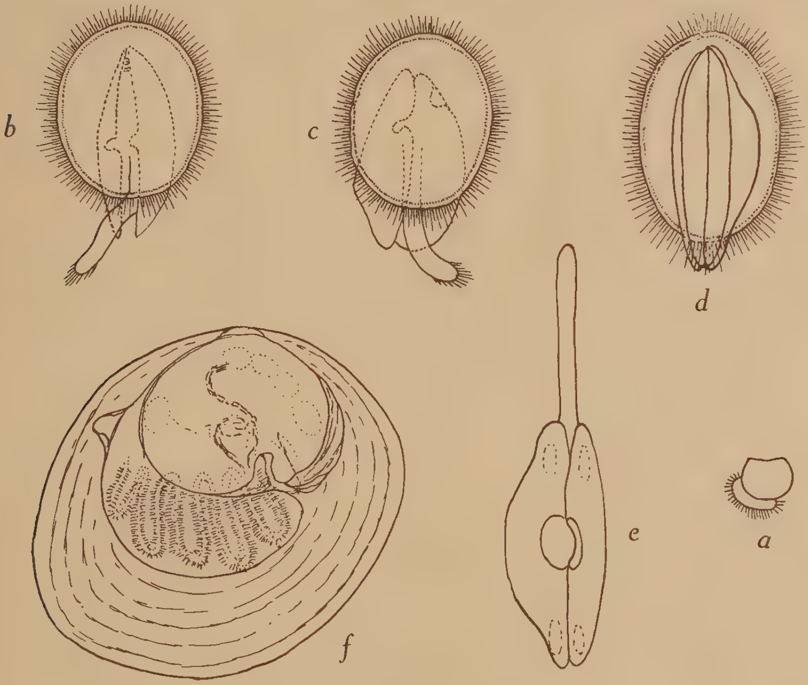


Fig. 6.

Heteranomia squamula.

a, early shelled larva from fertilization, 0·05 mm. long; *b*, *c*, later larvae, from plankton, swimming, 0·18 mm. long; *d*, late veliger, from plankton, ready to metamorphose, 0·2 mm. long; *e*, newly metamorphosed *Heteranomia*, grown in plunger-jar from planktonic veliger, 0·2 mm. long; *f*, young grown from planktonic veliger in plunger-jar, 0·45 mm. long.

Another species belonging to the family, which has a much less conspicuous pedal sinus, also occurs in the plankton. This resembles Odhner's specimen from Rovigno and may be *Anomia ephippium*.

THE LARVAE AND POST-LARVAE OF *MYSELLA BIDENTATA* AND A CLOSELY RELATED SPECIES

Certain large veligers often occur in the plankton, which when reared in plunger-jars grew into a species of *Mysella*. It was at first thought that these were *M. bidentata*; but another larva which was much less symmetrical was found which grew up into this species, and in shell gravel near the Eddystone all stages were found. As the first larva certainly belongs to the Montacutidae and the post-larva does not agree with other known species of *Mysella* or *Montacuta* it seems that there is a second species of *Mysella* occurring at Plymouth which is closely related to *Mysella bidentata* but distinct from it. Both species have the typical median cartilage with the lateral teeth forming a V enclosing it; the mantle is fringed with short processes, the siphons are hardly perceptible, the foot is large and very contractile and the posterior end of the shell is shorter than the anterior. The last character is much more marked both in the larva and post-larva of *M. bidentata*. The larva of the other form, here called *Mysella* sp., is nearly round, but slightly longer than broad, and the post-larva is oval with the posterior portion only slightly shorter than the anterior.

The larvae are comparable with the large veligers of *Kellia suborbicularis* (Lebour, 1938) and it is an interesting fact that the adults of both *Kellia* and of the known species of *Mysella* are viviparous, giving out their young as shelled larvae and yet attaining a large size before settling down.

Miyazaki (1936*a*) has described the larvae of *Mysella japonica* (Yokoyama). This species is also viviparous, the newly freed larvae being 122 μ in length. The largest form reared was 306 μ in length and this is very much like the Plymouth species at that stage. The same worker also reared another mollusc which he found commensal with the crustacean *Gebia major*. This he names *Erycina* sp. It is also viviparous, the larva at extrusion being 220 μ in length and beginning to lose the velum at 351 μ. It is thus seen that all these closely related genera apparently grow to a large size before settling down and that they probably remain a considerable time as planktonic veligers.

Mysella bidentata (Montagu) (Figs. 7 *a–c*)

Lovén (1848) has described and figured the newly ejected shelled larvae of this species, which are very like those of *Kellia* but slightly larger. The late larvae in the plankton, occurring chiefly from autumn to spring, are very flat and although nearly circular in outline have the anterior portion longer than the posterior. The velum is about the same size across its longest diameter as the shell. When ready to metamorphose the shell is 0·34 mm. long, with the lateral teeth already formed in a V and about four gill slits (Fig. 7 *a*). Slightly larger post-larvae were 0·4 mm. long and more oblique (Fig. 7 *b*). Young specimens about 0·5 mm. long had the adult form with the anterior end very much elongated. At a length of about 0·80 mm. the siphon and mantle processes were formed, and the teeth and cartilage were typical (Fig. 7 *c*).

Mysella sp. (Figs. 7 *d–g*)

Adults of this species have not yet been found, but young forms grown up from the plankton in plunger-jars show decided differences from the preceding species, the veliger differing much in form. Veligers from about 0·2 to 0·32 mm. across are very common in the plankton, especially in late summer and autumn, but they may also be found in spring. The velum is large and oval, reaching as far as the shell length (Figs. 7 *d*, *e*). At about 0·32 mm. the larva loses the velum (Fig. 7 *f*). The shell is very round in outline, the younger specimen being slightly longer than broad and at the time of metamorphosis both anterior and posterior ends are almost equal. Grown in plunger-jars these post-larvae grew into oval young with the posterior end rather shorter than the anterior and the mantle edged with fine processes (Fig. 7 *g*). The cartilage

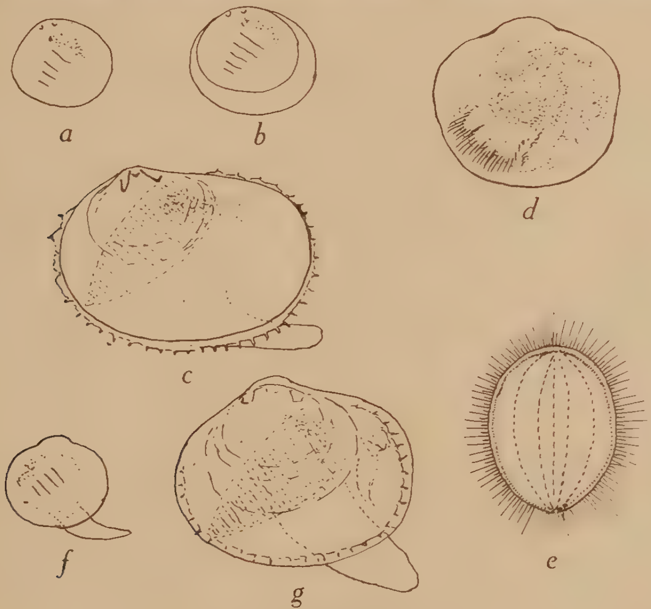


Fig. 7.

a–c, *Mysella bidentata.*

a, late veliger from plankton, 0·34 mm. long; *b*, post-larva from shell gravel, 0·4 mm. long; *c*, young from shell gravel, 0·82 mm. long.

d–g, *Mysella* sp.

d, *e*, veliger of *Mysella* sp. from plankton, 0·2 mm. long; *f*, newly metamorphosed form reared from planktonic veliger in plunger-jar, 0·32 mm. long; *g*, young reared from planktonic veliger in plunger-jar, 0·80 mm. long.

is well formed as well as the lateral teeth, the latter being blunter than those of *M. bidentata* and not forming such a distinct V. The foot is more pointed than in that species.

It was noticed in specimens of *Montacuta substriata* (Montagu) that the embryonic shell, visible in the adults, measured about 0·20 mm. in length, again showing a probable tendency to a large veliger in a viviparous form.

REFERENCES

Drew, G. A., 1901. The life history of *Nucula delphinodonta* (Mighels). *Quart. Journ. Micr. Sci.*, N.S., Vol. xliv, pp. 313–91.

Haas, F., 1929, 1937. *Klassen und Ordnungen des Tierreichs. Bivalvia*, i, pp. 1–984; ii, pp. 1–208.

Kändler, R., 1926. Muschellarven aus dem Helgolander Plankton. *Wiss. Meeresuntersuch.*, Bd. xvi (5), Abt. Helgoland, pp. 1–8.

Lebour, M. V., 1921. The food of young clupeoids. *Journ. Mar. Biol. Assoc.*, Vol. xii, pp. 458–67.

—— 1922. The food of plankton organisms. *Journ. Mar. Biol. Assoc.*, Vol. xii, pp. 644–77.

—— 1927. Studies of the Plymouth Brachyura. I. The rearing of crabs in captivity with a description of the larval stages of *Inachus Dorsettensis*, *Macropodia longirostris* and *Maia squinado*. *Journ. Mar. Biol. Assoc.*, Vol. xiv, pp. 795–814.

—— 1937. Larval and post-larval *Lima* from Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xxi, 2, pp. 705–10.

—— 1938. The life history of *Kellia suborbicularis*. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 447–51.

Lovén, G., 1848. Beiträge zur Kenntnis der Entwicklung der Mollusca. Acephala Lamellibranchia. *Abhandl. K. Schwed. Ak. Wiss.* 1848. (Republished in 1879 at Stockholm with additional notes, pp. 1–39.)

Matthews, A., 1913. Notes on the development of *Mytilus edulis* and *Alcyonium digitatum* in the Plymouth Laboratory. *Journ. Mar. Biol. Assoc.*, Vol. ix, pp. 557–60.

Miyazaki, I., 1935. On the development of some marine bivalves, with special reference to the shelled larvae. *Journ. Imp. Fisher. Inst.*, Vol. xxxi, No. 1, pp. 1–10.

—— 1936*a*. On the development of some marine bivalves, with special reference to the shelled larvae. II. *Journ. Imper. Fish. Inst.*, Vol. xxxi, No. 2, pp. 35–41.

—— 1936*b*. On the development of bivalves belonging to the genus *Corbicula*. *Bull. Jap. Soc. Sci. Fisheries*, Vol. 5, No. 4, pp. 249–54.

Odhner, N. H., 1914. Notizen über die Faune der Adria bei Rovigno. Beiträge zur Kenntnis der Marinen Molluskenfauna von Rovigno in Istrien. *Zool. Anz.*, Bd. xliv, Heft 2, pp. 145–70.

Pelseneer, P., 1926. Notes d'embryologie malacologique. Ponte et développement de *Cypraea europaea*, *Triforis perversa* et *Lucina lactea*. *Bull. Biol. France et Belg.*, Tome lx, pp. 88–112.

Sigerfoos, C. P., 1908. Natural history, organization and late development of the Teredinidae or Ship-worms. *Bull. Bur. Fish. Washington*, Vol. xxvii, pp. 191–231.

Thorson, G., 1935. Biologische Studien über die Lamellibranchier *Modiolaria discors* L. und *Modiolaria nigra* Gray in Ostgrönland. *Zool. Anz.*, Bd. cxi, Heft 11–12, pp. 297–304.

Winckworth, R., 1932. The British Marine Mollusca. *Journ. Conch.*, Vol. xix, No. 7, pp. 211–52.

ON THE NEMATOCYSTS OF HYDROMEDUSAE

By F. S. Russell, F.R.S.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–88)

In view of the possible use of nematocysts as characters for showing phylogenetic relationships among medusae (Weill, 1934), or even for the differentiation of species (Papenfuss, 1936), it is desirable that our knowledge of the nematocysts of medusae should be increased. I have accordingly examined the nematocysts in a number of species of Hydromedusae occurring at Plymouth.

Examination was always made on living material from which the portions to be examined, such as tentacles and mouth lips, were dissected. The dissected parts were placed on microscope slides, sometimes in sea water and sometimes in distilled water, and various stains such as magenta, methylene blue, and neutral red were used. Generally it was found that magenta and distilled water produced the best results for showing the minute structure of the nematocyst. The proportions of the nematocyst were first drawn under a monocular microscope with a camera lucida, and the slide was then transferred to a Leitz binocular microscope for more detailed examination. A 2 mm. apochromatic oil immersion objective was used, with × 10 eyepieces. Illumination was obtained with a "pointolite" and increased definition was helped by the use of a substage screen—a Wratten filter, Rheinberg No. 2 Blue Disc.

It is necessary to emphasize that observations were made on fresh material, since, as pointed out by Weill (1934, p. 30), fixation or desiccation may modify the form of the nematocyst. The nematocysts of most medusae are very small, the majority being less than 15μ in length, and certain difficulties may be experienced. One of the chief dangers is that if insufficient material is examined one type of nematocyst, at least, may be overlooked. I have on several occasions found an additional type of nematocyst, which I had not observed when examining previous medusae of the same species. This is generally due to the fact that different types of nematocysts may resemble one another in outline when in the undischarged* state. Unless, therefore, a very large number of nematocysts are discharged, that type which happens to be the least frequent may easily be overlooked if none are discharged. It was, for instance, only after I had examined a number of specimens of *Phialidium hemisphericum* that I found a few atrichous nematocysts among the very abundant mastigophores and later found that they were quite common.

---

* The terms discharged and undischarged are used here in preference to exploded and unexploded.

Considerable difficulty was also experienced in this species, as in some other Leptomedusae, in deciding whether the nematocysts were microbasic mastigophores or basitrichous haplonemes, i.e. whether the basal portion of the discharged thread was thicker than the remainder of the thread. A number of *Phialidium* were examined at different times and the conclusion was reached that, immediately after the discharge of the nematocyst the basal portion of the thread was considerably thicker than the terminal portion. But there was often subsequent swelling of the terminal portion, whether through increased pressure of the coverglass, or for other reasons, and the terminal portion assumed the same thickness as the basal portion. There must, therefore, always be some doubt whether the classification of some Leptomedusan nematocysts into microbasic mastigophores and basitrichous haplonemes is reliable. A similar increase in diameter in the terminal portion of the thread is referred to on page 151 in the microbasic euryteles of *Zanclea costata*, and it was noticed in other species. Weill (1934, pp. 58, 153) says that the diameter of the thread can only be accurately seen after staining with neutral red, but I found that this frequently caused swelling.

Difficulties of rather a similar nature arose concerning the microbasic mastigophores of *Leuckartiara octona*. Weill (1934, p. 392) records that he only found microbasic mastigophores in this species. In the first specimens that I saw, however, there was no doubt that all the discharged nematocysts seen were not mastigophores but microbasic euryteles. But, on examining more specimens, I found some microbasic mastigophores, and I was then in some doubt whether these might not really have been microbasic euryteles in which the basal portion was abnormal and had not swollen to its full extent, or whether perhaps the nematocysts were incompletely developed. These doubts were enforced when I found among the microbasic euryteles of *Rathkea octopunctata* some in which the walls of the base were parallel, and also some intermediate stages between this and the typical euryteles. A subsequent examination of more *Leuckartiara* showed that, in this species at any rate, the mastigophores were of a very slightly different shape from the euryteles and could eventually be distinguished in the undischarged state.

It was found that in one species, *Amphinema dinema*, one of the nematocyst types was present in the medusa just liberated from the hydroid, but absent in the adult medusa. The newly liberated medusa possessed microbasic euryteles and desmonemes; the adult had only microbasic euryteles. The hydroid had, however, both kinds of nematocysts, and it is probable that the nematocysts of the hydroid migrate into the developing bud and that the medusa itself when liberated is only capable of making one kind. How exactly the desmonemes disappear in the medusa is uncertain, but it is just possible that they remain throughout the life of the medusa and were not noticed owing to their numbers being swamped by those of the nematocysts made by the medusa as it grew.

Another possibility of error is due to the occurrence in a medusa of nematocysts which are not its own. I have on several occasions found, in the manubrium and hollow basal portions of the tentacles, nematocysts of quite a different type from those typical of the species of medusa in question. Thus I have seen large stenoteles in both *Leuckartiara octona* and *Amphinema dinema*. These must undoubtedly have been ingested by the medusa with its food. Usually these foreign nematocysts are obvious on account of their collapsed condition, but if they have been recently ingested they may lead to a source of error.

The nematocysts typical of any one species of medusa sometimes showed considerable differences between their range of size from one specimen to another. This is probably usually a function of the size, or age of the medusa, or its state of nourishment. For instance, the microbasic euryteles in *Amphinema dinema* just liberated from its hydroid were $6–7 \times 2\,\mu$, whereas in the adult medusa they were $7–9{\cdot}5 \times 2–3{\cdot}5\,\mu$; in one specimen of *Saphenia* the basitrichous haplonemes were mostly $18–19\,\mu$ long, while in another specimen they ranged from 22 to $28\,\mu$ long.

In the following pages accounts are given of the nematocysts from twenty species of medusae. In this paper I have followed Weill's classification, which, in spite of such difficulties as I have mentioned above, is extremely serviceable. It is quite to be expected that with the great variety of structure shown by coelenterate nematocysts it is impossible to make a rigid classification and intergrading types are sure to be found (e.g. Weill, 1934, p. 59). But on the whole his classification does enable one quickly to place a nematocyst in its right category. I feel, however, a little doubtful about trying to discriminate between homotrichous and heterotrichous forms in such small nematocysts as those of most medusae. It should be realized that in the minute structure of many of these nematocysts we are reaching the limit of comfortable visual observation. It thus becomes extremely difficult, and perhaps impossible, to decide the comparative lengths of the smaller spines or barbs owing to the effects of foreshortening when each spine is lying in a different plane. I have therefore purposely omitted any reference to homotrichy or heterotrichy in the following accounts, since I was never able to satisfy myself as to their validity.

In the following descriptions I have generally given only the types of the nematocysts and their measurements and location. It seemed unnecessary to attempt to describe in words their various shapes, when this has been shown in the accompanying figures. As I have already stated, the outlines of these figures were drawn with a camera lucida, but in order to eliminate personal error in the interpretation of the minute structure in the discharged nematocysts I have, for almost every drawing, called upon the help of independent observers who checked my drawings against the originals. For their kind assistance in this way I have especially to thank Mr E. Ford, Mr W. J. Rees and Mr G. M. Spooner.

As far as I could see, the number of spirals, when these occurred, on all the nematocysts examined was always three; this is in agreement with the statements of most workers. I have, however, in some drawings, where the basal portion of the thread was very narrow, only indicated the general appearance, as it was difficult to draw three spirals without spoiling the effect by running the lines together. In the accompanying figures all nematocysts, except where stated otherwise, are drawn to the same scale, so that the sizes of the nematocysts of the different species can easily be compared.

Measurements are only given to 0·5 μ on account of the difficulty of making sure that the nematocysts were exactly orientated horizontally and showing their greatest width. Any attempt to do this by pressure is liable to distort the capsule.

No attempt has been made to depict accurately the course of the thread in the undischarged basitrichous haplonemes or mastigophores. They are shown merely as simple coils, whereas they are generally thrown into S-shaped loops. While the capsules are mostly drawn in lateral view, the coils thus shown give the impression produced when the capsule is looked at dorso-ventrally.

This work must be regarded merely as a preliminary survey of the types of nematocyst present. No attempt has been made to obtain average sizes for the different species; this would involve measurements on great numbers of medusae of different sizes.

ANTHOMEDUSAE

Steenstrupia nutans (M. Sars).

There appear to be at least four kinds, stenoteles, ? anisorhize heterotrichous haplonemes, ? microbasic mastigophores or microbasic euryteles, and desmonemes (Figs. 1–7).

Stenoteles: there is a large range of size shown by these nematocysts, which appear to be grouped roughly in two sizes:

Large: 11–16 × 9–13 μ undischarged, 11–13 × 9–11 μ discharged.

Small: 7–10 × 6–8 μ undischarged.

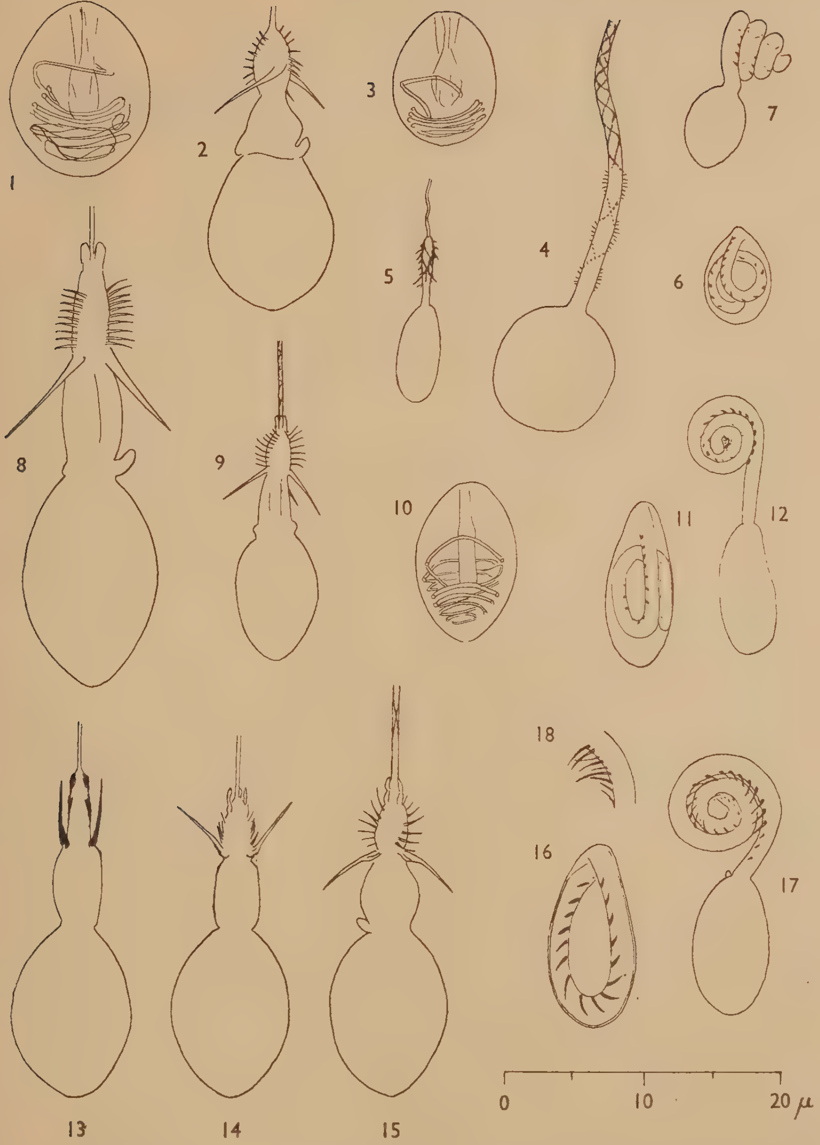
? *Anisorhize:* 11–12 × 9·5–10 μ undischarged, 9 × 8 μ discharged.

While these appeared to be anisorhize after first discharge, the thread later swelled up. There were definite spirals of short spines at the base, but the spirals on the rest of the thread appeared to have no spines.

? *Euryteles:* 8–12 × 3·5 μ undischarged.

I had the same difficulty with these as in *Rathkea*; in some specimens they appeared as euryteles and in others as mastigophores.

Desmonemes: 6–7·5 × 4·5–5·5 μ undischarged.



Figs. 1–7. *Steenstrupia nutans*: 1–3, stenoteles; 4, anisorhize; 5, ? eurytele; 6, 7, desmonemes. × *ca.* 2000.

Figs. 8–12. *Sarsia eximia*: 8, large stenotele from hydroid; 10, small stenotele from hydroid; 9, stenotele from newly liberated medusa; 11, 12, desmonemes from newly liberated medusa. × *ca.* 2000.

Figs. 13–18. *Purena gemmifera*: 13–15, stenoteles in process of discharge; 16, 17, desmonemes; 18, enlarged portion of desmoneme thread. × *ca.* 2000.

Sarsia eximia Allman.

In the hydroid I only found one kind of nematocyst, viz. stenoteles. In the newly liberated medusa there were, however, two kinds, stenoteles and desmonemes (Figs. 8–12).

HYDROID (*Syncoryne eximia*):

Stenoteles: these are of two sizes:

Large: 21·5–26 × 15–18 μ undischarged.

Small: 12–13 × 7·5–9 μ undischarged.

MEDUSA, newly liberated:

Stenoteles: these ranged in size from 9·5–16 × 6·5–10 μ undischarged. Most were *ca.* 13 × 9 μ undischarged; the smaller nematocysts may not have been fully developed.

Desmonemes: 9·5–12 × 4–5·5 μ undischarged. Most were *ca.* 12 × 4·5 μ undischarged.

I do not agree with Weill (1934, p. 385) as regards the structure of the stenoteles. I have discussed this below under *Purena gemmifera*.

Purena gemmifera Forbes.

Two kinds, stenoteles and desmonemes (Figs. 13–18).

Stenoteles: these are of two sizes:

Large: 16 × 12 μ undischarged.

Small: 13 × 9–10 μ undischarged.

Desmonemes: 13–14 × 6–7 μ undischarged.

While I agree with Weill (1934, p. 384) as regards the types of nematocysts present in this medusa, I cannot agree with him as regards the structure of the stenoteles in this species and in *Sarsia eximia*. Weill states that the small median spines are absent. They are in fact present and the stenotele is quite typical. The appearance or absence of the median spines is I think entirely due either to incomplete discharge of the nematocyst or to the incomplete development of the nematocyst. For instance, in a preparation in sea water and methylene blue, almost all the stenoteles were partially discharged with their posterior spines directed forwards. I was only able to find two fully discharged. In another preparation in distilled water and magenta, however, many were fully discharged with their basal spines directed backwards. In these the median spines were quite distinct. If the nematocysts are only partially discharged, the median spines all lie directed forwards over one another and each spiral appears only as a dark line. I have illustrated the various stages of discharge in Figs. 13–15. In many instances the whole armature of the hamp was broken away from the nematocyst, indicating that the nematocyst was not completely developed and the walls of the hamp had not reached their full thickness and strength.

Zanclea costata Gegenbaur (?).

I have examined a number of specimens newly liberated from the hydroid in the laboratory. The hydroid was the same as that described by Russell & Rees (1936). There were three kinds of nematocysts, stenoteles, macrobasic telotrichous euryteles and ? atrichous haplonemes.

Stenoteles: 7–13 × 6–12 μ undischarged, 6–11 × 5–9 μ discharged. These were present in the exumbrellar armature.

Macrobasic euryteles (Figs. 19–22):

Capsule: 7–7·5 × 4·5–5·5 μ undischarged, 5–6 × 3–4 μ discharged.

Length of hamp: *ca.* 25–30 μ discharged.

Ampulla: 4·5–5 × 1·5–2·5 μ.

The three spirals of barbs were present *on* the ampulla and extended for a short way down the hamp as in *Pteroclava krempfi* (Weill, 1934, p. 78). When first discharged the thread beyond the hamp is definitely thinner than the hamp itself. The thread, however, swells up later under pressure to the same thickness as the hamp. This increase in thickness of the thread under pressure possibly accounts for the differences in the observations of Weill and Allman (Weill, 1934, p. 78 *et seq.*), but both these authors describe the ampulla in this much discussed species as having no barbs. Both Weill and Allman also give the length of the hamp as being much greater than in my specimens. These nematocysts occur in the cnidophores of the tentacles.

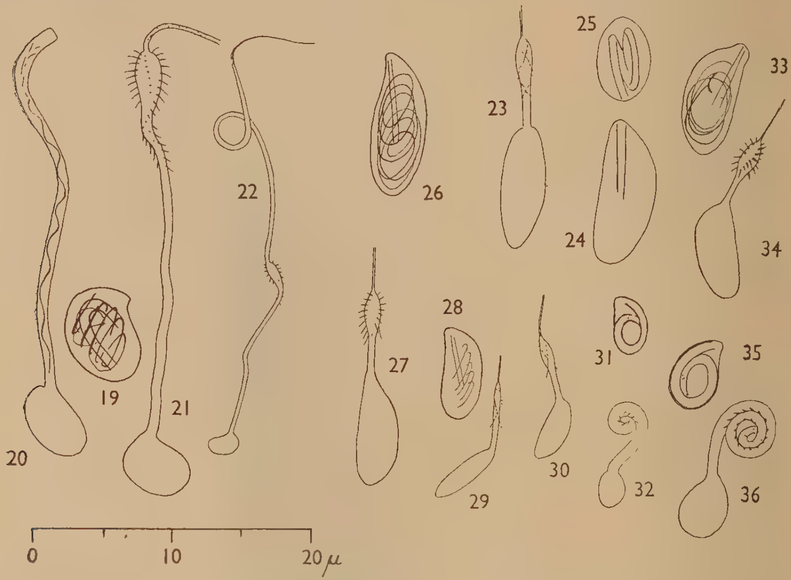
? *Atriches:* I only saw an occasional atriche and unfortunately obtained no measurements. They appeared to be extremely rare.

While discussing the nematocysts of *Zanclea* it will be convenient to answer a question raised by Weill (1936*a*) and Ranson (1937) concerning the nature of the exumbrellar nematocyst armature. The four exumbrellar groups of nematocysts are embedded in solid tissue and not in hollow sacs. This agrees with Weill's observation (1934, p. 420) on the American medusa. Allman (1871, p. 224) states that the nematocysts are immersed in a clear fluid; they certainly have this appearance unless highly magnified.

A comparison between the American medusa as described by Weill (1934, p. 418) and the Plymouth medusa as described by Russell & Rees (1936) is given below. Both descriptions refer to medusae just liberated from the hydroid:

	Plymouth	Woods Hole
Size	0·6–0·7 mm. high	1·8 mm. high
Cnidophores	18–20 × 13 μ	30 × 17 μ
Stenoteles	7–13 × 6–12 μ	12–17 μ
Euryteles	Telotrichous	Merotrichous
Capsule	7–7·5 × 4·5–5·5 μ	9 μ
Hamp	25–30 μ long	79 μ long
Ampulla	4·5 × 5 μ long	7 μ long

It can only remain a matter of opinion whether these differences should be regarded as of specific value, until a large number of medusae with two and four tentacles from different localities have been examined. Until we know what degree of constancy there is in these differences, any further discussion is at present valueless, but it should be borne in mind that mere size difference is of doubtful value.



Figs. 19–22. *Zanclea costata*, newly liberated: 19–21, macrobasic euryteles, × *ca.* 2000; 22, macrobasic eurytele after pressure, × *ca.* 900.

Figs. 23–25. *Bougainvillia britannica*: 23, 24, microbasic euryteles; 25, desmoneme (dorsal view). × *ca.* 2000.

Figs. 26–32. *Rathkea octopunctata*: 26, 27, microbasic euryteles from oral tentacles; 28, 30, microbasic euryteles from marginal tentacle; 29, ? microbasic mastigophore; 31, 32, desmonemes. × *ca.* 2000.

Figs. 33–36. *Lizzia blondina*: 33, 34, microbasic euryteles; 35, 36, desmonemes. × *ca.* 2000.

Bougainvillia ramosa (van Beneden).

One adult male only examined (2·2 mm. diameter).

Two kinds: microbasic euryteles and desmonemes.

Euryteles: 8–9 × 3·5–4 μ undischarged.

Desmonemes: 4·5–5·5 × 3–3·5 μ undischarged.

These nematocysts were similar in shape and appearance to those of *Lizzia blondina* (Figs. 33–36).

Bougainvillia britannica Forbes.

Two kinds, microbasic euryteles and desmonemes (Figs. 23–25).

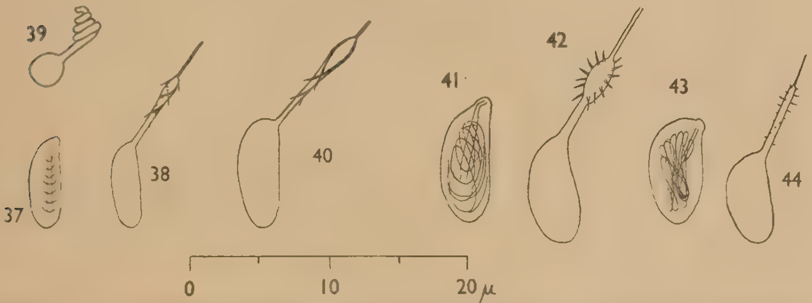
Euryteles: 10–11 × 3·5–4 μ undischarged, 9 × 3 μ discharged.

Desmonemes: 6–6·5 × 3·5–4 μ undischarged.

Of these the euryteles only occur in the mouth tentacles; both kinds of nematocysts are found in the marginal tentacles, the desmonemes being the more abundant.

Lizzia blondina Forbes.

Two kinds: microbasic euryteles and desmonemes (Figs. 33–36).
Present in marginal tentacles and mouth tentacles:
Euryteles: 7–10 × 3–5 μ undischarged, 6–7·5 × 2·5–3·5 μ discharged.
Present in tentacles only:
Desmonemes: 4·5–6 × 2·5–3·5 μ undischarged.



Figs. 37–40. *Amphinema dinema*: 37, 38, microbasic euryteles from hydroid; 39, desmoneme from hydroid; 40, microbasic eurytele from medusa. × *ca.* 2000.

Figs. 41–44. *Leuckartiara octona*: 41, 42, microbasic euryteles; 43, 44, microbasic mastigophores. × *ca.* 2000.

Rathkea octopunctata (M. Sars).

Two kinds: microbasic euryteles and desmonemes (Figs. 26–32).
Present in marginal tentacles and oral tentacles:
Euryteles:
In oral tentacles: 10–12 × 3–4 μ undischarged, 8–9 × 2·5–3·2 μ discharged.
In marginal tentacles: 6–10·5 × 2·5–4 μ undischarged (mostly 6–8 μ), 5–7·5 × 1·5–3 μ discharged.
Present in marginal tentacles only:
Desmonemes: 3–5 × 2–3 μ undischarged.

Sometimes the microbasic euryteles appear as microbasic mastigophores (Fig. 29). This was especially so in one specimen in which the majority appeared to be microbasic mastigophores.

Amphinema dinema (Pér. & Les.).

In the hydroid and newly liberated medusa there are two kinds, microbasic euryteles and desmonemes. In the adult medusa there is only one kind, microbasic euryteles (Figs. 37–40).

HYDROID.

Euryteles: 6·5–7·5 × 2–2·5 μ undischarged.

Desmonemes: 3·5–4·5 × 2–2·5 μ undischarged, 2·5 × 2 μ discharged.

MEDUSA.

Newly liberated:

Euryteles: 6–7 × 2 μ undischarged.

Desmonemes: 3·5–4 × 2 μ undischarged.

Adult:

Present in marginal tentacles and mouth lips.

Euryteles: 7–9·5 × 2–3·5 μ undischarged, 6·5–7·5 × 2–2·5 μ discharged.

Amphinema rugosum (Mayer).

One specimen *ca.* 2 mm. high only seen. There was only one kind, microbasic eurytele (not figured).

Euryteles: 8–9 × 2 μ undischarged.

Leuckartiara octona (Fleming).

There appear to be quite definitely two kinds, microbasic euryteles and microbasic mastigophores (Figs. 41–44).

Present in tentacles and mouth lips:

Euryteles: 8–10·5 × 3–4·5 μ undischarged.

Present (?) only at base of tentacles or on umbrella margin:

Mastigophores: 7 × 3·5–4 μ undischarged.

At first I thought that there were only euryteles present, but subsequent examinations showed that there were undoubtedly also mastigophores, but these were much fewer. They appeared as small groups, and I was unable to make certain whether they were limited to the base of the tentacle or the umbrella margin. They were certainly not present in the main body of the tentacle. The mastigophores are shorter and more plump than the euryteles.

Weill (1934, p. 392) states that in *L. octona* from Wimereux there were only microbasic mastigophores, 10–12 μ long, present in the tentacles and mouth lips.

Willia stellata Forbes.

I have unfortunately been unable to obtain any living specimens of this interesting medusa. I have, however, had its hydroid, *Lar sabellarum*, and its nematocysts are sufficiently interesting to be described here. There were three kinds, macrobasic mastigophores, microbasic euryteles and desmonemes (Figs. 45 *a–j*).

Mastigophores: 24–33 × 9–13 μ undischarged.

In some specimens treated with acetic acid or distilled water the distal end of the hamp swelled into an ampulla, like that in the macrobasic eurytele of *Zanclea* (Fig. 45 *d*).

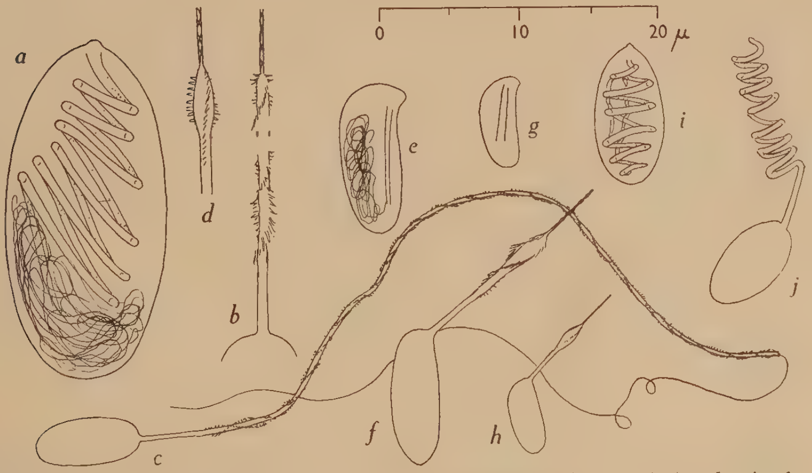
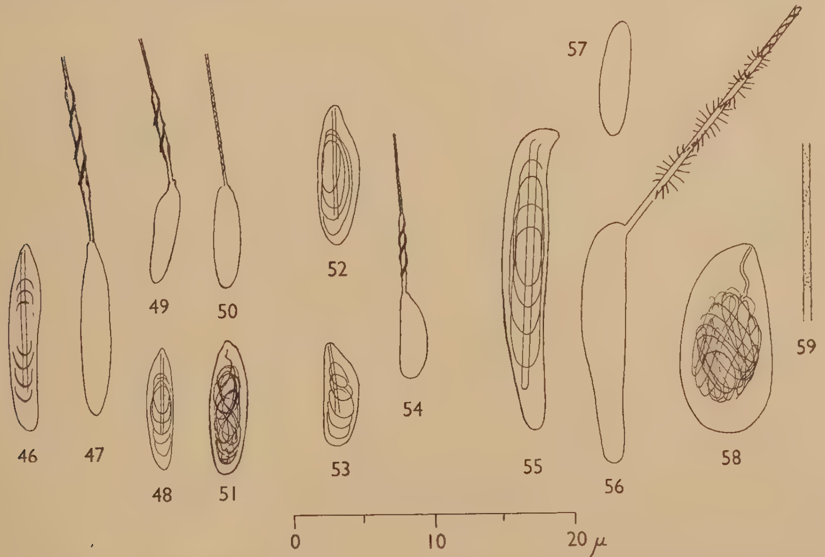


Fig. 45. *Lar sabellarum* hydroid: *a–d*, macrobasic mastigophores (*c*, × *ca.* 600); *e–h*, microbasic euryteles; *i–j*, desmonemes. × *ca.* 2000.



Figs. 46–51. *Phialidium hemisphericum*: 46, 47, large microbasic mastigophores from exumbrella; 48, 49, microbasic mastigophores from tentacle; 50, 51, atrichous haplonemes. × *ca.* 2000.

Figs. 52–54. *Phialella cymbaloides*: microbasic mastigophores. × *ca.* 2000.

Figs. 55–59. *Saphenia gracilis*: 55, 56, basitrichous haplonemes; 57, very small ? basitrichous haploneme from margin of umbrella; 58, atrichous haploneme, with portion of thread, 59. × *ca.* 2000.

Euryteles:

Large: 9–13 × 4–5 μ undischarged, 9·5–10 × 3–3·5 μ discharged.

Small: 6·5–7 × 2·5–3 μ undischarged, 5·5 × 2 μ discharged.

Desmonemes: 10 × 5 μ undischarged.

The desmonemes had unusually long threads for Anthomedusae, with as many as seven coils.

The macrobasic mastigophores were present only in the nematocyst pad on the proboscis.

LEPTOMEDUSAE

Mitrocomella brownei (Kramp).

One adult female only seen. There were two kinds, basitrichous haplonemes and atrichous haplonemes (Figs. 60–65).

Present in marginal tentacles and mouth lips:

Basitriches: two sizes.

Large: 14–16 × 4–5 μ undischarged, 13–14 × 3–3·5 μ discharged.

Small: 8·5–11 × 2–2·5 μ undischarged, 8–9 × 2 μ discharged.

Atriches: 11–12 × 4 μ undischarged, 10–11 × 3·5 μ discharged.

The armature on the base of the basitriches is very strong, the barbs being very long and pronounced.

Phialidium hemisphericum (L.).

There were two kinds, atrichous haplonemes and what appeared to be microbasic mastigophores. These were quite clearly mastigophores when first discharged, but, later, possibly due to pressure, the thread swells up so that they appear as basitrichous haplonemes (Figs. 46–51).

? *Mastigophores:* these were of two sizes:

Large: 12–14 × 2–3 μ undischarged, 11–13 × 1·5–2 μ discharged.

Small: 8–10 × 2 μ undischarged, 7 × 1·5 μ discharged.

The large mastigophores occurred on the umbrella. Some of the small mastigophores were mussel-shaped, but most were almond-shaped. The small ones were by far the most numerous.

Atriches: 9–10 × 2·5–3 μ undischarged.

It was only after I had examined a number of specimens that I found a discharged atriche. They can easily be confused with the others in their undischarged state, being of approximately the same size. In one of the later specimens I examined, when placed in distilled water and magenta, only the atriches discharged. They were then seen to be quite common, and were subsequently found in many specimens.

Weill (1934, p. 464) states that in this medusa from Wimereux there was only one type of nematocyst, a basitrichous haploneme, 10–12 μ long. He found, however, that in the hydroid of this species, *Clytia johnstoni*, there were both basitriches and microbasic mastigophores. It seems possible that he may have been misled by the swelling of the thread.

I examined medusae newly liberated from the hydroid and found both mastigophores and atriches present. In the hydroid I found mastigophores of two sizes but saw no atriches. I do not regard this as proof that they were not present.

When examining the mastigophores in this species and in *Phialella cymbaloides* I could never see for certain whether the spirals on the hamp were composed of spines. I imagined that this was so, for at the end of each dark diagonal line there was a slight projection. This may, however, have been an optical illusion due to the continuation of the spiral round the hamp. There are three spirals present, but I have not indicated these in Figs. 47 and 49 because it would not have been possible to draw them satisfactorily to so small a scale. I have therefore shown the appearance of the hamp when the upper surface is brought into focus. Thus in the small nematocysts there appear to be two dark diagonal lines and in the large nematocysts three diagonals.

Phialella cymbaloides (van Beneden).

One kind: ? microbasic mastigophores or basitrichous haplonemes (Figs. 52–54). I experienced the same swelling of the thread in these as in *Phialidium*. There were two sizes.

Small, in marginal tentacles: 6–9 × 2–3 μ undischarged.

Large, in mouth lips: 9–13 × 2·5–4 μ undischarged.

It is curious that I saw no atriches, for these seem to be present in most Leptomedusae.

Eucheilota clausa (Hincks).

There appear to be two kinds, atrichous haplonemes and possibly basitrichous haplonemes (Figs. 66–74). As with *Phialidium hemisphericum*, however, the basitriches in at least one specimen appeared as microbasic mastigophores immediately after discharge.

? *Basitriches:* these nematocysts occurred in two distinctly different shapes, (i) in the shape of an almond; (ii) in the shape of a mussel, *Mytilus*.

The almond-shaped basitriches were of two sizes and occurred in the tentacles and mouth lips: 12–19 × 3–4 μ undischarged, and 6·5–10·5 × 1·5–3 μ undischarged. The smaller of these were more numerous in the mouth lips than the larger.

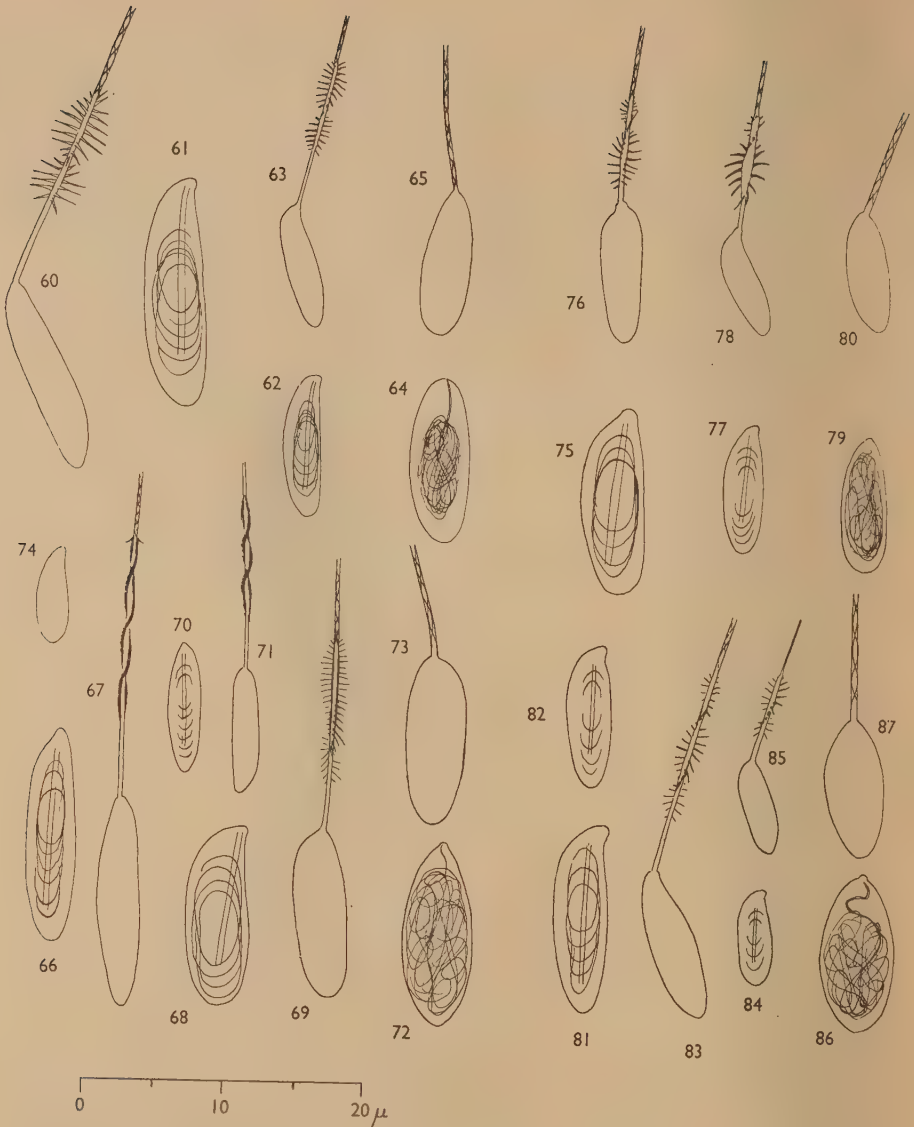
The mussel-shaped basitriches appeared to be confined to the umbrella margin and had longer barbs on their basal armature.

Atriches: ca. 12–13 × 4–5 μ undischarged.

Saphenia gracilis (Forbes & Goodsir).

There were three kinds, basitrichous haplonemes and atrichous haplonemes, and very small ? haplonemes or mastigophores (Figs. 55–59).

Basitriches: these were of two sizes.


60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
0
10
20 μ

Figs. 60–65. *Mitrocomella brownei*: 60–63, basitrichous haplonemes; 64, 65, atrichous haplonemes. × *ca.* 2000.

Figs. 66–74. *Eucheilota clausa*: 66–71, ? basitrichous haplonemes; 68, 69, mussel-shaped form; 72, 73, atrichous haploneme; 74, very small ? basitrichous haploneme. × *ca.* 2000.

Figs. 75–80. *Helgicirrha schulzei*: 75–78, basitrichous haplonemes; 79, 80, atrichous haplonemes. × *ca.* 2000.

Figs. 81–87. *Octorchis gegenbauri*: 81–85, ? microbasic mastigophores; 86, 87, atrichous haplonemes. × *ca.* 2000.

Large, in marginal tentacles: 18–28 × 3–4 μ undischarged.
Small, in mouth lips: 10–13 × 2·5–3 μ undischarged.
Atriches: 12–16 × 4–7 μ undischarged.

The very small nematocysts, 7–8 × 2–2·5 μ undischarged, were present on the umbrella margin. Unfortunately I was unable to see any discharged, so could not make certain of their type.

Weill (1934, p. 460) states that in *S. gracilis* from Wimereux there were two kinds, atriches 15 × 7 μ and basitriches 22 × 5 μ.

Octorchis gegenbauri Haeckel.

Two kinds, atrichous haplonemes and basitrichous haplonemes, the smaller of which may have been basitrichous mastigophores (Figs. 81–87).

Basitriches: these were of two sizes in the tentacles and margin:
Large: 12–15 × 3·5–5 μ undischarged.
Small: 7–8·5 × 2–2·5 μ undischarged.
In the mouth lips I saw only one size, 8·5–10 × 2·5–3 μ undischarged.
Atriches: 9–13 × 4–5·5 μ undischarged.

I could not make out for certain whether the smaller basitriche nematocysts were haplonemes or mastigophores.

Helgicirrha schulzei Hartlaub.

Two kinds: basitrichous haplonemes and atrichous haplonemes (Figs. 75–80).

Basitriches: 9–13·5 × 3–4 μ undischarged.
Atriches: 9–12 × 3–4 μ undischarged.

All types were present in the tentacles but I could see only small basitriches in the mouth lips.

SIPHONOPHORA

Muggiaea atlantica Cunningham.

On the tentilla there are three kinds, desmonemes on the terminal filament, and large microbasic mastigophores and atrichous haplonemes in the battery (Figs. 88 *a–f*).

Desmonemes: 7–10 × 4–6 μ undischarged.
Mastigophores: 36–43 × 6–7·5 μ undischarged, 33–36 × 6 μ discharged.
Atriches: 13–18 × 3–4 μ undischarged (often anisorhize in form).

Interspersed among the desmonemes on the terminal filament there are numerous so-called "anacrophores", 5–6 × 2 μ, arranged in pairs much as Weill (1934, fig. 111) has shown for *Diphyes spiralis*. Since the desmonemes show a range in size down to that of the "anacrophores" I am inclined to think that the "anacrophores" may be immature desmonemes at the stage before they become rounded; otherwise it is difficult to understand whence so many desmonemes originate. Similarly I observed that the immature atrichous

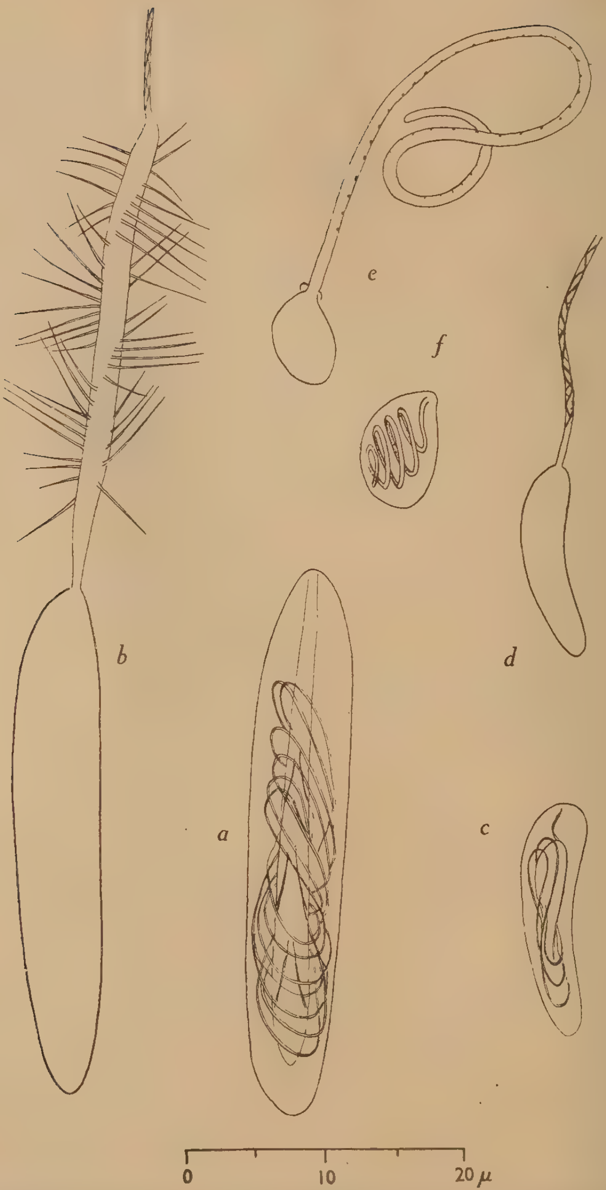


Fig. 88. *Muggiaea atlantica*: *a*, *b*, microbasic mastigophores; *c*, *d*, atrichous haplonemes; *e*, *f*, desmonemes (*e*, thread uncoiled). × *ca.* 2000.

haplonemes, 9–12 × 2 μ, would partly discharge and appear like "anacrophores", having a dilated basal portion with a terminal filament from the end of which the remaining un-everted portion of the thread could be traced back to the capsule in which it was coiled. On these grounds I suggest that the so-called "acrophores" and "anacrophores" recorded in Siphonophores may be merely stages in the development of other nematocysts.

Discussion

The nematocysts may be regarded as characters of a medusa worthy of description, just as much as any of the other structures which are dealt with when a detailed description is made of any one species. But, apart from this aspect, it has been repeatedly urged that a knowledge of their structure may give a clue to the phylogenetic relationships of species of coelenterates whose relationships are not made clear by other known characters (e.g. Stephenson, 1929; Weill, 1934). With this further addition to our knowledge of the nematocysts of medusae, it is therefore not without interest to summarize the results for medusae alone, as Weill has done for so many groups. I have therefore given a table (p. 163) showing the distribution of the different types of nematocysts among a number of species of Anthomedusae and Leptomedusae. In this table a cross in brackets indicates that I was uncertain to which category a nematocyst should belong; the two alternative categories are therefore shown in this manner whenever I was in doubt. The medusae have been arranged in their order of classification into the different families that are more generally accepted at the present time.

A first glance at this table shows that most of these medusae fall into four main groups as regards their nematocyst characters. Of these the first, the Tubulariidae, are set apart by having four types of nematocysts.

The other three groups comprise the Corynidae and Eleutheriidae in which there are two kinds, desmonemes and stenoteles; the Clavidae and Bougainvilliidae or Margelidae with two kinds, desmonemes and microbasic euryteles; and thirdly the Leptomedusae as a whole which have two kinds, atrichous haplonemes and the basitrichous haploneme—microbasic mastigophore type (except *Phialella cymbaloides*). There is yet a fifth group, the Pandeidae, whose adults lack all types of nematocysts except the microbasic eurytele, with the addition of a microbasic mastigophore in *Leuckartiara*.

It can thus be seen that the distribution of nematocyst types fits very well with the accepted classification of the medusae based on other characters. Some reliance may therefore be placed on them as classificatory characters. Their value has been shown quite definitely for *Zanclea* and the Eleutheriidae by Weill (1934, 1936*b*). *Zanclea* has indeed been set apart from the Corynidae on account of its very remarkable tentacle structure and because its gonads do not surround the manubrium. Yet its hydroid is very corynid in appearance. Its nematocysts show its relationship with the tubularian and corynid groups in the stenoteles. It is separated from them, however, by the absence of desmonemes, which occur in both the other groups, and by the presence of the remarkable macrobasic euryteles. The position of the Eleutheriidae has long been a source of discussion, but their nematocysts show quite clearly a close relation with the Corynidae.

When we consider the other groupings we see that the hydroid of *Willia stellata* stands apart in having macrobasic mastigophores which are not found in any of the other medusae. This is further evidence justifying the formation of a separate family, the Williidae, to hold this medusa and its near relatives. It is also of great interest to find that in its nematocysts this species shows a relationship with the clavid-bougainvilliid group in the presence of desmonemes and absence of stenoteles. It is thus in its relationship to this group somewhat like *Zanclea* in its relationship to the tubulariid-corynid group. Both species possess a unique type of nematocyst and both have somewhat remarkable armature on the exumbrella. *Willia* shows no relationship to the Leptomedusae in its nematocysts and is thus probably correctly placed in the Anthomedusae.

There are other points of interest shown in the table, such as the apparent relationship between *Rathkea* and *Lizzia* and *Bougainvillia*, but until more species are studied it seems a little premature to discuss such relationships in detail.

It is a noticeable feature that while the Anthomedusae are thus divided into a number of distinct groups by their nematocyst characteristics, the Leptomedusae as a whole show no such division (cf. Weill, 1934, p. 478). This is in agreement with the great diversity of form shown by the Anthomedusae as compared with the Leptomedusae. It is unfortunate, because I had hoped that by examining a number of widely separated genera of Leptomedusae some of their relationships might have been shown by their nematocysts.

This preliminary review of medusan nematocysts has shown that the opinion that their study may be of value in showing phylogenetic relationships is justified and that more observations should be made. When we consider their value as specific characters, however, it is evident that a great deal more research will have to be done on the dimensions and variations of the nematocysts in individual species. It is true that a study of the accompanying illustrations of the nematocysts of Leptomedusae shows that a few of them are quite distinctive, but on the whole they are extraordinarily alike. All the species so far studied are quite easily distinguishable by other morphological characters, and the value of nematocysts as specific characters will have to be shown in species that are closely alike and in which as yet specific distinctions remain in considerable doubt. Typical examples of such medusae are the species of *Obelia* and of *Aequorea*. I have not myself examined such species yet. If the differences are small, as they are quite likely to be, it is necessary for the observer to have had considerable experience in observing

	Desmonemes	Haplonemes			Heteronemes				Stenoteles
		Atrichous	Basitrichous	Anisorhize	Microbasic mastigophores	Macrobasic mastigophores	Microbasic euryteles	Macrobasic euryteles	
ANTHOMEDUSAE									
Tubulariidae									
Steenstrupia nutans	×	..	..	×	(×)	..	(×)	..	×
*Ectopleura dumortieri**	×	..	..	×	×	..	..	..	×
Corynidae									
Sarsia eximia	×	..	..	..	..	..	..	..	×
*Sarsia prolifera**	×	..	..	..	..	..	..	..	×
Purena gemmifera	×	..	..	..	..	..	..	..	×
Eleutheriidae									
Eleutheria dichotoma†	×	..	..	..	..	..	..	..	×
Cladonema radiatum†	×	..	..	..	..	..	..	..	×
Pteronemidae									
Zanclea costata?	..	×	..	..	..	..	..	×	×
Clavidae									
*Oceania armata**	×	..	..	..	..	..	×	..	..
Bougainvilliidae-Margelidae									
Bougainvillia ramosa	×	..	..	..	..	..	×	..	..
Bougainvillia britannica	×	..	..	..	..	..	×	..	..
Lizzia blondina	×	..	..	..	..	..	×	..	..
Rathkea octopunctata	×	..	..	..	..	..	×	..	..
Pandeidae									
Amphinema dinema	‡	..	..	..	..	..	×	..	..
Amphinema rugosum	..	..	..	..	..	..	×	..	..
Leuckartiara octona	..	..	..	..	×	..	×	..	..
Williidae									
Willia stellata (Hydroid)	×	..	..	..	..	×	×	..	..
LEPTOMEDUSAE									
Mitrocomidae									
Mitrocomella brownei	..	×	×	..	..	..	..	..	..
Eucopidae									
Phialidium hemisphericum	..	×	(×)	..	(×)	..	..	..	..
Phialella cymbaloides	..	..	(×)	..	(×)	..	..	..	..
Eucheilota clausa	..	×	(×)	..	(×)	..	..	..	..
Saphenia gracilis	..	×	×	..	..	..	..	..	..
Octorchis gegenbauri	..	×	×	..	..	..	..	..	..
*Eirene viridula**	..	×	..	..	×	..	..	..	..
Helgicirrha schulzei	..	×	×	..	..	..	..	..	..
Aequoridae									
*Aequorea forskalia**	..	×	×	..	(×)	..	..	..	..

* Weill (1934). † Weill (1936*b*). ‡ Present only in medusa just liberated from hydroid.

nematocysts. Only then will he know what kind of differences to look for. Examination of closely related species must, also, be made by the same observer. There is liable to be a pronounced personal factor in observing these minute structures under high powers of the microscope. On this account interpretations of structure may be quite different by different observers, because the same kinds of nematocysts may appear so different unless examined in exactly the same positions. In this respect it seems rather significant that when I compare my results with those of so eminent a specialist as Dr Robert Weill I find that I differ from his conclusions in no less than five out of the six species that we have both studied.

SUMMARY

The nematocysts of twenty species of Hydromedusae occurring at Plymouth are described. Of these, twelve were Anthomedusae and seven were Leptomedusae, and one was the Siphonophore, *Muggiaea atlantica*. The medusae fit very well into the generally accepted classification as regards the types of nematocysts they possess.

Lar sabellarum, the hydroid of *Willia stellata*, has a type of nematocyst not found in the other species—a macrobasic mastigophore. This is a further justification for the formation of a separate family, the Williidae, to hold this species and its relations.

While the Anthomedusae are clearly split up into distinct groups as regards their types of nematocysts, the Leptomedusae form a single group.

It is suggested that the so-called acrophores and anacrophores recorded in siphonophores may be merely stages in the development of other nematocysts.

It is urged that much more research is required on variation in size and structure of nematocysts in individual species before they can be used as specific characters for separating doubtful species.

REFERENCES

ALLMAN, GEORGE JAMES, 1871–2. A monograph of the gymnoblastic or tubularian hydroids. *Ray Society*, pp. 1–450.

PAPENFUSS, EMMA JOHNSTONE, 1936. The utility of the nematocysts in the classification of certain Scyphomedusae. I. *Lunds Universitets Årsskrift*, N.F., Avd. 2, Bd. 31, Nr. 11, 26 pp. (*Kungl. Fysiograf. Sällsk. Handl.*, N.F., Bd. 46, Nr. 11.)

RANSON, G., 1937. Cnidactine et cnidothylacies chez les Anthoméduses. *Bull. Soc. Zool. France*, Tome LXII, pp. 318–29.

RUSSELL, F. S. & REES, W. J., 1936. On rearing the hydroid *Zanclea implexa* (Alder) and its medusa *Zanclea gemmosa* McCrady, with a review of the genus *Zanclea*. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 107–29.

STEPHENSON, T. A., 1929. On the nematocysts of sea anemones. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 173–200.

WEILL, ROBERT, 1934. Contribution à l'étude des cnidaires et de leurs nématocystes. I. Recherches sur les nématocystes (Morphologie—Physiologie—Développement). II. Valeur taxonomique du cnidome. *Trav. Stat. Zool. Wimereux*, Tome X, pp. 1–347 and Tome XI, pp. 349–701.

—— 1936*a*. Au sujet de la définition et de la validité du genre *Güntherella* Weill 1934 (Hydrozoaires). *Bull. Soc. Zool. France*, Tome LXI, pp. 526–32.

—— 1936*b*. Le cnidome des Cladonémides *Eleutheria dichotoma* et *Cladonema radiatum*, son cycle et son interprétation. *C.R. Acad. Sci., Paris*, Tome 203, pp. 816–18.

LUCERNARIA DISCOIDEA, A NEW SPECIES FROM THE CHANNEL ISLANDS

By N. B. Eales, D.Sc.

University of Reading

(Text-figs. 1–3)

While collecting on the *Zostera* beds at Grève d'Azette, Jersey, on August 23 1937 Mr R. B. Pike found fourteen specimens of an unknown lucernarian. These *Zostera* beds, made famous by the work of Mr J. Hornell, are now greatly impoverished, and at extreme low tide during the spring tide period only a few scattered patches of the weed remain. Hornell reported *Haliclystus octoradiatus* from this area, and it was while searching for it that the present species was found.

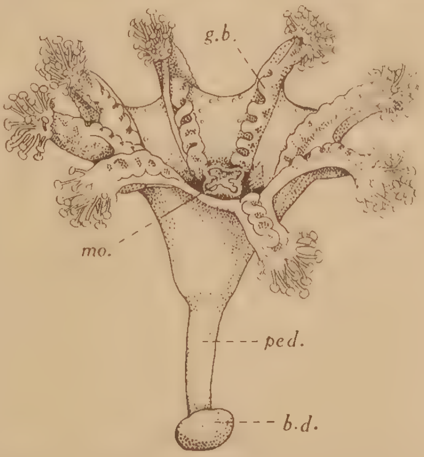


Fig. 1. *Lucernaria discoidea* n.sp.; an individual of medium size in lateral view. × 5. *b.d.* basal disk; *g.b.* genital band; *mo.* mouth; *ped.* peduncle.

The general form of the lucernarian is typical (Fig. 1), but more delicate than that of *L. campanulata*. When alive, the colour was greenish yellow, with numerous scattered, pale yellow, opaque spots all over the umbrella, and a few cerulean blue spots between the genital bands not far from the mouth. The yellow and blue colour rapidly disappeared in formalin. The specimens vary in size from 5 to 20 mm. high, and from 3 to 15 mm. across the bell. The basal disk is distinct and is broader than the peduncle, which is rather long and slender, and expands gradually into the umbrella. Of the fourteen specimens, one has twelve arms, twelve have eight arms, and one has seven arms, the odd arm in the last specimen being formed by the fusion of two arms. The normal number can therefore be taken as eight. In a fully expanded specimen the length of the free arm is about one-third of the radius of the umbrella, and the tentacles which crown the arm are the distinguishing feature of the species. In all other species of both *Lucernaria* and *Haliclystus* which I have been able to trace, the tentacles are rounded and button-like (capitate) at the tips, the nematocysts being confined to this area. In the species here described the fully formed tentacle has a *flat disk* at its apex, although young tentacles show that the discoid type is derived from the normal rounded one and the disk can be contracted to form a thick "cake". The number of tentacles in a bunch rarely exceeds twenty-five and is usually fewer (Fig. 2). Though all are slender, the size and shape vary, and three kinds can be distinguished:

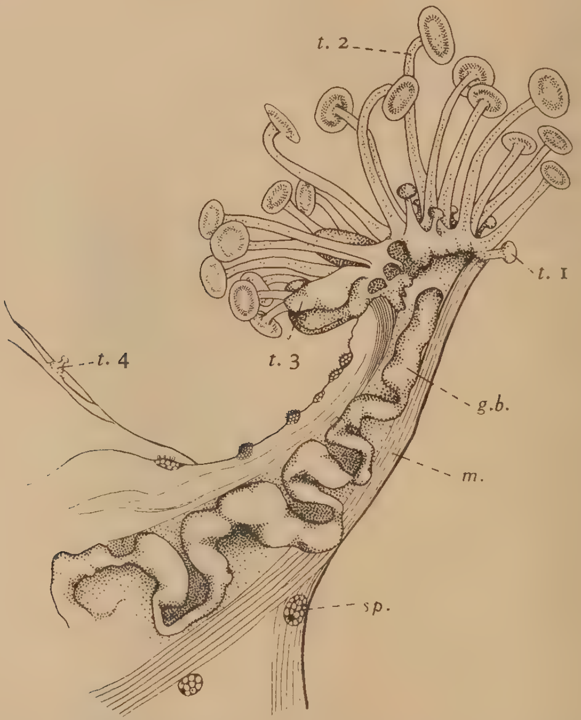


Fig. 2. The arm of *L. discoidea* n.sp. from the oral side. Its apex is twisted to the right to expose the aboral glandular tentacles. ×25. *g.b.* genital band; *m.* muscle; *sp.* opaque spot on umbrella; *t.* 1, capitate tentacle; *t.* 2, discoid tentacle; *t.* 3, glandular discoid tentacle; *t.* 4, vestigial per- or interradial tentacle.

(*a*) On the oral side of the arm are from four to six short capitate tentacles (Fig. 2, *t.* 1).

(*b*) On the extremity of the arm are situated about ten or twelve long slender tentacles, with disk-shaped heads set at right angles to the centrally placed stalk, somewhat like the podia of an *Echinus* (Fig. 2, *t.* 2).

(*c*) On the aboral side of the summit of the arm are from three to five tentacles with discoid heads, and rather short stalks expanded greatly on the aboral side of the base to form glandular adhesive organs. A bulbous prolongation of each swollen area is contained within the arm (Fig. 2, *t.* 3).

The cruciform mouth with frilled lips projects on a short manubrium from the centre of the umbrella, and is held in place by four perradial strips fastened to the umbrella between the adradially situated genital bands, as the latter diverge towards the arms. The interradial areas being free from such attachment are usually more widely expanded, so that the genital bands naturally fall into four groups of two each, although symmetry is regained on the umbrella margin. (Cf. *L. quadricornis*, where the arms are grouped in twos.) The genital bands are of characteristic shape, being sinuous and swollen, but continuous. They extend as far as the base of the tentacles, and appear to possess one aperture for each band near the tip. The gastric filaments are unbranched, the stalk is one-chambered, but four bands run downwards as continuations of the taenioles. On the inner surface of the disk these bands broaden out, are visible externally, and have the shape of a four-rayed clover-leaf.

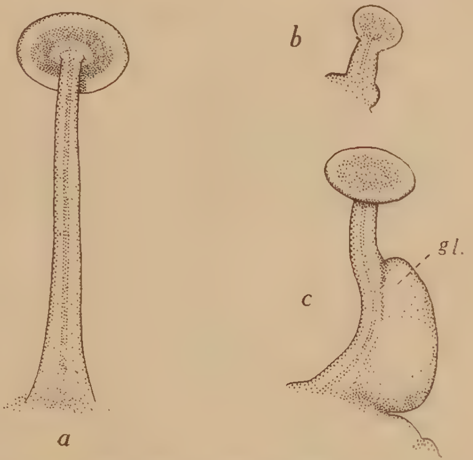


Fig. 3. Three types of tentacle from the arm of *L. discoidea* n.sp. × 60. *a*, tall discoid; *b*, short capitate; *c*, short glandular discoid: *gl.* glandular base of tentacle.

Young specimens exhibit two points of difference from adults. The tentacles tend to resemble the ordinary capitate type, and there is in some a single capitate tentacle on the umbrella edge in the centre of each bay between the arms. In older specimens these isolated perradial and interradial tentacles become reduced in size and may either disappear or persist in one or more of the bays. Elmhirst (1922) noted similar tentacles in *L. quadricornis*.

Although *L. discoidea* is here called a new species, it was discovered over eighty years ago by H. Milne Edwards at Langrune, east of Cherbourg, and accurately figured by him in the Disciples' Edition of Cuvier's *Règne Animal*, 1847. He found orange and greenish specimens, and gave a coloured figure of the former. He noted both the knob-shaped and disk-shaped tentacles, the opaque spots on the umbrella, the sinuous nature of the genital bands, the simple gastric filaments, and the swollen basal expansions of the peduncle supports. He did not see, however, the adhesive pads on the outer tentacles, or the attachment of the mouth angles. His specimens did not possess the blue spots. At the time two species of lucernarian were known, viz. Müller's *L. auricula* and *L. quadricornis*, the former a *Haliclystus* and the latter a *Lucernaria*. Milne Edwards called his specimens *L. auricula*, an obvious error in the light of present-day knowledge, since his specimens had no colletocystophores and Müller's had. Consequently a specific name is required for it, and *L. discoidea* is suggested, because of the peculiarity of the tentacles.

Specimens have been deposited in the British Museum of Natural History, and I should like to thank Dr A. K. Totton for his assistance with the literature, and Mr Pike for drawings of the animal.

REFERENCES

BROWNE, E. T., 1910. Coelentera. V. Medusae. *Rept. Nat. Antarct. Exped. Nat. Hist.*, Vol. 5, pp. 1–62, Pl. 1–7.

CARLGREN, O., 1930. Die Lucernariden. *Further Zool. Results Swedish Antarct. Exped.*, Vol. II, No. 4, p. 18.

—— 1935. Über eine neue Südafrikanische Lucernariide, *Depastromorpha africana* n.gen., n.sp., nebst Bemerkungen über den Bau und die Systematik dieser Tiergruppe. *K. Svenska Vet. Akad. Handl.*, Ser. III, Vol. 15, No. 1, 24 pp.

CLARK, H. J., 1878. Lucernariae and their Allies. Washington, Smithsonian Institution.

EDWARDS, H. MILNE, 1847. *Le Règne Animal* (Cuvier, Disciples' Edition, 1838–49), p. 111 and Pl. 63.

ELMHIRST, R., 1922. Notes on *Lucernaria quadricornis* Müller, and related Species. *Ann. Mag. Nat. Hist.*, Vol. 10, 9th ser. pp. 221–4.

HAECKEL, E., 1879. *System der Medusen.* Jena, pp. 1–672.

MÜLLER, O. F., 1806. *Zoologica Danica.* Havniae, p. 35, Pl. 152.

UCHIDA, T., 1929. Studies on the Stauromedusae and Cubomedusae, with special reference to their metamorphosis. *Jap. Journ. Zool. Tokyo*, Vol. II, pp. 103–89.

UCHIDA, T. & HANAOKA, K., 1933. On the morphology of a stalked medusa, *Thaumatoscyphus distinctus* Kishinouye. *Journ. Fac. Sci. Hokkaido Imp. Univ.*, Ser. 6, Zool. Vol. 2, pp. 135–53.

—— —— 1934. Anatomy of two stalked medusae with remarks on the distribution of the Stauromedusae in Japan. *Journ. Fac. Sci. Hokkaido Imp. Univ.*, Ser. 6, Zool. Vol. 2, pp. 211–38.

SALT ERROR IN DETERMINATIONS OF PHOSPHATE IN SEA WATER

By L. H. N. Cooper, D.Sc., F.I.C.

Assistant Chemist at the Plymouth Laboratory

Investigations extending over several years have shown that the salt error in colorimetric determinations of phosphate in sea water may be dependent, not only upon the concentrations of reagents and to some extent on the temperature, but also on the method of making the comparison. Uncertainty had become acute since alterations in procedure had been made, which were found to invalidate comparison between results obtained before and after 1933. Since we possess much the longest series of phosphate records yet made and these show promise of close correlation with other biological phenomena, it became essential to ensure that all were on a comparable basis.

The Conditions of Formation of Phosphomolybdenum Blue

From a detailed study Tischer (1934) concluded that:

(1) To reduce one molecule of phosphomolybdic acid to phosphomolybdenum blue four stannous ions are required.

(2) The experimental solution should lie between 0·09 and 0·17N H_2SO_4. This agrees with Kalle's finding (1934), since 100 ml. of water treated with 1 ml. of the usual acid molybdate reagent contains 0·14N H_2SO_4. The optimum normality of acid is very dependent on the amount of molybdate present (cf. Kalle, 1934).

(3) The influence of pH is due to its effect on the competing oxidation-reduction systems, phosphomolybdic acid $\rightleftharpoons$ phosphomolybdenum blue, $Sn^{++++} \rightleftharpoons Sn^{++}$ and $H^+ \rightleftharpoons H$. Electrometric measurements showed that the colour intensifying effect of sulphate is due to an increase in the pH of the reaction mixture.

(4) The depth of colour in distilled water, reached after thirty minutes, is independent of temperature but electrolytes give rise to a temperature coefficient.

(5) Chloride, in contrast to sulphate, causes not only a diminution but also an alteration in the shade of the reduced solution so complicating the salt error problem in work with sea water (cf. also Robinson & Wirth, 1935).

Formation of Complex Molybdenyl Halides

Reduction of molybdic acid in solution in strong hydrochloric or hydrobromic acid, either with hydrogen iodide or electrolytically at a platinized platinum electrode, leads to the formation of complex molybdenyl halides,

$R_2 [MoOX_5]$, where R is an alkali metal or an ammonium base and X is chlorine or bromine. Under suitable conditions these complexes may be crystallized, the chlorides being green and the bromides brown to yellow. They are all rapidly hydrolysed by water, the concentrated solutions being reddish brown passing through orange to bright yellow on dilution. The bromides are even more liable to hydrolysis than are the chlorides. The stages in the hydrolysis have been elucidated (James & Wardlaw, 1927; Angell, James & Wardlaw, 1929). This work agrees with the views put forward by Tischer (1934). In a sample of sea water submitted to colorimetric analysis of phosphate we have all the conditions required for the formation of these complexes—large amounts of chloride and some bromide, excess of molybdic acid, a degree of acidity sufficient to promote their formation and a reducing agent, present only in small quantity it is true, but more powerful than hydrogen iodide.

This formation of molybdenyl halides and their yellow hydrolytic products may be readily shown by adding a solution of stannous chloride, drop by drop, to a resting sample of sea water containing acid molybdate reagent. Bright yellow streaks will be seen slowly falling towards the bottom of the flask. Complete suppression of the complex molybdenyl halide formation is difficult, but it may be much reduced by rotating the solutions rapidly whilst the stannous chloride solution is being added, so avoiding a temporarily high local concentration of the reducing agent. It may also be reduced by cutting down the amount of stannous chloride added (Atkins, 1928 p. 202). Controls are necessary to ensure that this is not cut down too much.

Between five and ten minutes after the addition, a slight development of yellow tint need not prevent an experienced analyst making a reproducible colour match. Since the yellow colour then develops more rapidly, comparison after half an hour or more is undesirable.

When colour filters are used a very serious source of error may arise. The formation of molybdenyl chlorides is accompanied by absorption not only in the blue and green but also in the red. This absorption in the red would be attributed to the presence of phosphate. In any one group of experiments where "yellowing" is taking place, it may be uniform and very difficult to detect by ordinary methods of control, using a photometer in a dimly lit room. When this happens the results may appear excellent; the colour increment for the addition of a given amount of phosphate may be uniform throughout a long series of determinations; blank measurements may appear in perfect order, and yet the content of phosphate found may be as much as 75% too high. The unsuitability of the solutions for analysis is at once evident when they are examined in bright daylight. The colour increment is also greater than is found when a good blue has developed.

Strength of Molybdate Reagent

Kalle (1933, 1934, 1935 *a*, *b*) has made a detailed investigation of the optimum conditions for the analytical determination of phosphate in artificial sea water. He found (1934) that the usual molybdate reagent is blended in the right proportions, but that if the amount used were reduced by one-half the intensity of colour development was always increased and the salt error diminished. From Kalle's results with the Pulfrich photometer (S72 filter), using 1 ml. of molybdate reagent per 100 ml. of water, a correction factor, 1·13, was found, and agreed closely with determinations then made by the writer using Hehner cylinders and natural sea water—1·11 and 1·12.

The reduced quantity of molybdate reagent (1 : 100) was adopted as standard practice in April 1934, but comparison in Hehner cylinders was continued in preference to the Pulfrich photometer.

The Effect of Copper

Subsequently Kalle (1935 *a*) suggested that minute traces of copper affect the development of blue colour and are mainly responsible for the salt error. To overcome this he suggested adding copper to all standards and sea water samples, so that results would then not require correction for salt error. Tischer and Kalle agree that the depressing effect of increasing quantities of copper is represented by a curve with a flat inflection but do not agree as to its position. They both used 1 ml. of molybdate reagent per 100 ml. of water. The flat part of the curve, where increase in the amount of copper leads to no further decrease in colour, lies between 120 and 1200 mg./m.^{3} according to Kalle and between 1460 and 8560 mg./m.^{3} according to Tischer. With 250 mg./m.^{3}, the decrease in colour in distilled water is about 3% according to Tischer, about 5% according to Kalle and about 10% according to extensive experiments made by the writer. It is clear from Tischer's discussion that the effect of copper will be the greater the less the quantity of stannous chloride used.

As much copper as 30 mg./m.^{3} has been shown to have a negligible effect on colour development by Tischer, Kalle and the writer. With this the investigations of Robinson & Wirth (1935) and Brambel & Cowles (1937) agree. Such an amount of copper has never been found in our distilled water nor in our sea-water samples, so that we feel that no phosphate analyses here are likely to be affected in this way. Since our Nansen-Pettersson sampling bottle is made of a copper alloy which has corroded badly, a number of tests have been made for contamination of the samples by copper. During the few minutes of a routine haul from less than 100 m. contamination is not serious, but when water had been left in the sampling bottle for four hours during the journey back to the laboratory it was found to have been enriched with 500 mg./m.^{3} Thus in working at greater depths or with less attention to washing the bottle with fresh water after the day's work, there is an ever present risk of serious contamination. The alloy used in the hydrographical bottles is unsatisfactory and an effort should be made to build them of incorrodible components such as stainless steel and ebonite, or silver-lined bottles of the *Discovery* Expedition type should be used.

From June 1936 to October 1937 copper was added to all our standards and sea-water samples prior to analysis (25 μg. Cu and 1 ml. of molybdate reagent per 100 ml.). The development of colour was diminished but to the same extent in both sea water and standards (Tables I and II). The phosphate results required the same correction factor as though no copper had been added.

DETERMINATION OF SALT ERROR

The method of phosphate analysis is that of Denigès as applied to sea water by Atkins (1923). The reagent blank, which includes colour due to impurities in the reagents, natural colour of the water and any colour due to slight reduction of molybdic acid in absence of phosphate, was evaluated as described by Cooper (1933, p. 715).

TABLE I. EFFECT OF COPPER ON SALT ERROR CORRECTION FACTOR.

Waters compared (D.W. = distilled water; S.W. = sea water)		Comparison by daylight in Hehner cylinders		Comparison with S filter in Pulfrich photometer	
		No. of Determinations	Mean Factor	No. of Determinations	Mean Factor
		2 ml. molybdate reagent/100 ml.			
D.W. + no added Cu	D.W. + 4 mg.-atom/m.^{3} added Cu	—	—	2	1·15
D.W. + no added Cu	S.W. + no added Cu	2	1·36	2	1·23
D.W. + no added Cu	S.W. + 4 mg.-atom/m.^{3} added Cu	—	—	1	1·25
D.W. + 4 mg.-atom/m.^{3} added Cu	S.W. + 4 mg.-atom/m.^{3} added Cu	1	1·25(?)	2	1·13
		1 ml. molybdate reagent/100 ml.			
D.W. + no added Cu	D.W. + 4 mg.-atom/m.^{3} added Cu	—	—	9	1·11
D.W. + no added Cu	S.W. + no added Cu	3	1·11	5	1·07
D.W. + no added Cu	S.W. + 4 mg.-atom/m.^{3} added Cu	—	—	4	1·23
D.W. + 4 mg.-atom/m.^{3} added Cu	S.W. + 4 mg.-atom/m.^{3} added Cu	2	1·10	8	1·10

In certain experiments the amount of acid molybdate was reduced from 2 to 1 ml. per 100 ml. of water (cf. Kalle 1935*b*; Tischer 1934). No attempt was made exactly to control temperature. In winter during the day the laboratory temperature ranged from 11 to 15° C. During the experiments of June 1936 it was 17° C. The acid ammonium molybdate reagent was prepared as described by Atkins (1923). The solution of stannous chloride was freshly made by dissolving 0·10–0·15 g. $SnCl_2.2H_2O$ in 25 ml. 4*N* hydrochloric acid. A solution made by dissolving metallic tin in hydrochloric acid in presence of a little copper sulphate (Atkins 1923) is equally effective.

One drop of the stannous chloride solution added to 100 ml. of water containing 0·5 mg.-atom/m.^{3} P (15 mg./m.^{3} P) gives a sixfold excess of stannous ions. Stronger solutions of phosphate require more stannous chloride but the same amount must be added to standards as well. If there should be any doubt as to whether sufficient stannous chloride has been added, the increment of colour due to, say, 0·3 mg.-atom/m.^{3} P should be determined.

Direct visual comparison was usually made in Hehner cylinders 20 cm. high. In work with the Pulfrich photometer, absorption tubes 15 cm. long and holding about 90 ml. of liquid were used in conjunction with the red S72 filter. This shows maximum absorption above 700 mμ. (see Cooper and Milne, 1938, Fig. 1).

TABLE II. SALT ERROR CORRECTION FACTOR FOR PHOSPHATE IN SEA WATER UNDER DIFFERENT CONDITIONS OF DETERMINATION

Comparison by daylight in Hehner cylinders		Comparison in Pulfrich photometer with S72 filter	
Date	Factor	Date	Factor
I. Using 1 ml. of molybdate reagent per 100 ml. of water.			
(*a*) No copper added to either sea water or standard.			
June 1934*a*	1·11	Jan. 1936*a*	1.05
June 1934*b*	1·12	Jan. 1936*b*	1·09
March 1936	1·09	June 1936	1·13
Jan. 1938	1·15	Sept. 1936	(1·00?)
Feb. 1938	1·17	Jan. 1937	1·13
		Jan. 1938	1·11*
Mean	1·13		1·11
(*b*) 0·4 ml. *M*/1000 $CuSO_4$ added to sea water and standards.			
March 1936	1·09	Jan. 1936	1·13
Dec. 1937	1·10	Sept. 1936	1·04
		Jan. 1937	1·10
		Dec. 1937	1·10
Mean	1·10		1·10
II. Using 2 ml. of molybdate reagent per 100 ml. of water. No copper added to either sea water or standard.			
March 1936	1·37	June 1936	1·23
Feb. 1938	1·35	Jan. 1937	1·22
Mean	1·36		1·22

* Result of an experiment with extensive cross-checks and controls; has been given the weight of four experiments.

In Tables I and II are collected determinations of the correction factor for salt error in sea water under different experimental conditions; in Table III may be found those by other workers.

When 1 ml. of molybdate reagent is used per 100 ml. of water the method of comparison is immaterial. The correction factor, 1·12, has been adopted for all the writer's determinations with 1 ml. molybdate per 100 ml. of water, no matter whether comparison had been made by direct comparison of the blue colour in Hehner cylinders or by means of the red S72 filter in the Pulfrich photometer, or whether or not extra copper had been added to both sea water and standards.

However, when double the concentration of reagent is used (2 : 100, as in Atkins' original method), the correction factor is considerably greater for comparison by daylight (1·35) than when a red filter is used in some kind of photometer (1·19). It is evident that the spectral composition of the blue colour differs somewhat according to the amount of reagent used. The factor 1·35 has been adopted for correcting all direct visual determinations made by Atkins and the writer, using 2 ml. of molybdate reagent per 100 ml. of water.

TABLE III. CORRECTION FACTOR FOR SALT ERROR FOR SEA WATER OF $35\,{}^{\circ}/_{\circ\circ}$ SALINITY

Method	Author	
(*a*) When 2 ml. of acid molybdate reagent is used per 100 ml. of sea water.		Factor (*a*)
Spectrophotometer with filters having maxima at 660 and 684 mμ	Buch (1929)	1·17*
Photoelectric colorimeter; 650 mμ	Brambel & Clowes (1937)	1·17†
Pulfrich Photometer and S72 filter	Robinson & Wirth (1935)	1·15
” ” ”	Cooper (this paper)	1·22
Mean of measurements with filters		1·18
Comparison by daylight	Ibañez	1·29‡
” ” ”	Brujewicz & Krasnowa (1933)	1·35
” ” ”	Redfield, Smith & Ketchum (1937)	1·35
” ” ”	Cooper (this paper)	1·36
” ” ”	Igelsrud, Robinson & Thompson (1936)	1·25§
(*b*) When 1 ml. of acid molybdate reagent is used per 100 ml. of sea water.		Factor (*b*)
Pulfrich photometer and S72 filter	Kalle (1934)	1·13
” ” ” ”	Cooper (this paper)	1·11
Mean of measurements with filters		1·12
Comparison by daylight	Cooper (this paper)	1·13

* Buch found that the salt error varied with the concentration of phosphate. The figure given is taken from his Tables and graphs for amounts of phosphate up to about 1 mg.-atom m.^{3} P.

† From graph.

‡ For waters containing less than 1·1 mg.-atom/m.^{3} P.

§ For water of $29\,{}^{\circ}/_{\circ\circ}$ salinity.

Small variations in these factors arise from variations in the concentration of stannous chloride and in temperature. The correction factor must not be assumed to be a true constant. It is desirable therefore that each worker should establish the factor afresh for the precise conditions applying to his own work.

There is some evidence (Table I) that, when 2 ml. of molybdate reagent is used per 100 ml. the presence of copper (*ca.* 200 mg./m.^{3}) affects differentially the development of colour in distilled water standards and in sea water. In presence of copper the salt error factor for comparison by daylight may be about 1·25, but this figure is the result of one determination only.

Analyses here are now carried out by the procedure described by Wattenberg (1937), except that only 0·05 or 0·10 g. of stannous chloride dissolved in 25 ml. $4N$ hydrochloric acid is used since hydrolysis is thereby more completely suppressed. They are invariably made within 24 hours of collection.

SUMMARY

The yellowing which may occur during phosphate determinations in sea water is attributed to hydrolytic products of complex molybdenum halides.

When 1 ml. of the usual acid molybdate reagent is used per 100 ml. of water, addition of copper as recommended by Kalle reduces the development of colour in sea water samples and in distilled water standards to the same extent. The correction factor 1·12 applies to comparison by daylight in Hehner cylinders and to photometric determinations with a red filter.

When 2 ml. of reagent is used per 100 ml. of water, the factor depends on the method of comparison. With comparison by daylight in Hehner cylinders it is 1·35, whereas if a photometer with a red filter is used it is only 1·19.

REFERENCES

Angell, F. G., James, R. G. & Wardlaw, W., 1929. Complex bromides of quinquevalent molybdenum. *Journ. Chem. Soc.*, pp. 2578–89.

Atkins, W. R. G., 1923. The phosphate content of fresh and salt waters in its relationship to the growth of the algal plankton. *Journ. Mar. Biol. Assoc.*, Vol. XIII, pp. 119–50.

—— 1928. Seasonal variations in the phosphate and silicate content of sea water during 1926 and 1927 in relation to the phytoplankton crop. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 191–205.

Brambel, C. E. & Cowles, R. P., 1937. The photoelectric determination of phosphorus in estuarine waters. *Science*, Vol. 85, pp. 340–2.

Brujewicz, S. W. & Krasnowa, W. S., 1933. Cited by S. W. Brujewicz in *Methods of Chemical Oceanography* (in Russian), Moscow, 1933, p. 118.

Buch, K., 1929. Über die Bestimmungen von Stickstoffverbindungen und Phosphaten im Meerwasser. *Rapp. Proc.-Verb. Cons. Int. Expl. Mer*, Vol. LIII, pp. 36–52.

Cooper, L. H. N., 1933. Chemical constituents of biological importance in the English Channel. Pt. I. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 677–728.

Cooper, L. H. N. & Milne, A., 1938. The ecology of the Tamar Estuary. II. Underwater illumination. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 509–27.

Ibañez, O. G., 1933. Note on the effect of salts in the determination of phosphate in sea water by Denigès' method. *Journ. Cons. Int. Expl. Mer*, Vol. VIII, pp. 326–9.

Igelsrud, I., Robinson, R. J. & Thompson, T. G., 1936. The distribution of phosphate in the sea water of the north-east Pacific. *Univ. Washington Publ. Oceanogr.*, Vol. 3, No. 1, pp. 1–34.

James, R. G. & Wardlaw, W., 1927. Co-ordination compounds of quinquevalent molybdenum. *Journ. Chem. Soc.*, pp. 2145–56.

Kalle, K., 1933, 1934, 1935*a*, *b*. Meereskundliche chemische Untersuchungen mit Hilfe des Zeisschen Pulfrich-Photometers. II. Arbeitsweise. III. Methodische Untersuchung der Phosphatgehaltsbestimmung. IV. Der Einfluss chemischer Stoffe auf die Phosphatgehaltsbestimmung. V. Die Bestimmung des Gesamt-Phosphorgehaltes, des Plankton-Phosphorgehaltes (lebende Substanz) und Trübungsmessungen. *Ann. d. Hydrogr.*, Jahrg. LXI, pp. 124–8; LXII, pp. 65–74 and 95–102; LXIII, pp. 58–65, 195–204.

REDFIELD, A. C., SMITH, H. P. & KETCHUM, B., 1937. The cycle of phosphorus in the Gulf of Maine. *Biol. Bull.*, Vol. LXXIII, pp. 421–43.

ROBINSON, R. J. & WIRTH, H. E., 1935. Photometric investigation of the ceruleomolybdate determination of phosphate in waters. *Ind. Eng. Chem.* (*Anal.*), Vol. 7, pp. 147–56.

TISCHER, J., 1934. Über die Bestimmung des Phosphorsäure mittels der Phosphor-Molybdänblau-Methode und deren Anwendung auf Pflanzenaschen. *Zeits. Pflanzenernährung Düngung u. Bodenkunde*, Teil A, Bd. 33, pp. 192–242.

WATTENBERG, H., 1937. Critical review of the methods used for determining nutrient salts and related constituents in salt water. *Rapp. Proc.-Verb. Cons. Int. Expl. Mer*, Vol. CIII, pp. 1–26.

APPENDIX

On 13 April 1938, after this paper had been prepared, a fresh batch of acid molybdate reagent was made up. Using 1 ml. of this per 100 ml. of water, the salt error correction factor was found to be 1·39 instead of 1·12 as anticipated. Moreover the factor decreased with time:

April 14	1·39
April 19	1·33
May 13	1·29
June 8	1·29
July 24	1·25.

To remove a slight yellow tint, the 50% (by volume) sulphuric acid had been treated with a few drops of *N*/10 permanganate as suggested by Kalle (1934) (0·4 mg. Mn per litre of acid molybdate reagent). The resulting manganous salt, although very small, provided a possible explanation of the anomalous correction factor. To test this view, two fresh 400 ml. batches of acid molybdate reagent were prepared on July 28, one treated with permanganate as above, the other not. The same samples of ammonium molybdate and sulphuric acid were used as in April. The salt error correction factor, determined by direct visual comparison in Hehner cylinders, was, in each case, 1·11, in agreement with the value established on p. 176. The anomalous factor cannot therefore be attributed to the presence of manganese. Further search for the cause of the anomaly has not been made but, nevertheless, this experience emphasizes the need for care if accurate results are to be had.

REDEFINITION OF THE ANOMALY OF THE NITRATE-PHOSPHATE RATIO

By L. H. N. Cooper, D.Sc., F.I.C.

Assistant Chemist at the Plymouth Laboratory

The paper on the ratio of nitrogen to phosphorus in the sea (Cooper, 1937) was written before it was realized that in phosphate determinations, using *two* ml. of molybdate reagent per 100 ml. of water, the magnitude of the salt error correction factor is changed by the use of a spectral filter. Due to the resulting uncertainty it was felt better to use uncorrected figures for phosphate content rather than to risk a correction which might later prove to be wrong. We now know (Cooper, 1938) that the factor, 1·35, can be applied to all Plymouth data given in the 1937 paper and presumably to the results of the *Dana* and *Discovery II* there cited. The ideal ratio of 20 : 1, for nitrate-N/phosphate-P expressed as milligram-atoms, therefore becomes 20 : 1·35 = 14·8, or, say, 15 : 1. Most of Redfield's figures are probably amenable to the same correction. The revised nitrate-N/phosphate-P ratio agrees even better with the mean ratio of the thirteen sets of nitrogen and phosphorus analyses of plankton taken off Plymouth, viz. 16·3.

I suggest therefore that the "anomaly of the nitrate-phosphate ratio" be redefined as the amount by which the nitrate-phosphate ratio differs from fifteen, each salt being expressed in milligram-atoms and phosphate being corrected for salt error by the appropriate factor (see Cooper, 1938).

REFERENCES

Cooper, L. H. N., 1937. On the ratio of nitrogen to phosphorus in the sea. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 177–82.

—— 1938. Salt error in determinations of phosphate in sea water. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 171–8.

PHOSPHATE IN THE ENGLISH CHANNEL, 1933–8, WITH A COMPARISON WITH EARLIER YEARS, 1916 AND 1923–32

By L. H. N. Cooper, D.Sc., F.I.C.
Assistant Chemist at the Plymouth Laboratory

(Text-fig. 1)

Continued observations of dissolved inorganic phosphate at International Hydrographic Station E 1, 22 miles S. 37° W. from Plymouth, started by Atkins in 1923, support the accepted picture of the seasonal cycle (Matthews, 1917; Atkins, 1923–30; Harvey, 1928, 1934; Cooper, 1933*a*, *c*; Harvey *et al.*, 1935), but fresh points of interest have emerged, their significance lying in the contrast they offer to earlier years. Difficulties due to the uncertainty as to the salt error have now been overcome (Cooper, 1938).

Numerical records for phosphate have not been published for 1930, 1931, 1933 and 1937 whilst the results for January to April 9 1934, given in the *Bulletin Hydrographique*, have been corrected by too low a factor. Those for April 20–December 1934 and for 1935 and 1936 in that *Bulletin* are correct.

There is a strong case for publishing nutrient salt results in terms of the milligram-atom of the element concerned (Cooper, 1933*d*; Carter, Moberg, Skogsberg & Thompson, 1933), and this has been endorsed by a subcommittee of the International Council. The milligram-atom of phosphorus per cubic metre corrected for salt error has therefore been adopted as the unit of measurement for this paper and for future work here. To facilitate comparison all my results since 1930 for Station E 1 expressed in this unit are brought together in Table I. Each is corrected by the salt error factor appropriate to the conditions of analysis (Cooper, 1938). In 1938 and sometimes in earlier years, the factor has been accurately determined at the time of analysis. There must always be a little uncertainty unless the factors are so determined since they are not true constants. Records for Station E 2 are similarly presented in Table II.

The salt error correction factor for all Atkins' (1923, 1925, 1926, 1928, 1930) phosphate results is 1·35 so that, to convert these to mg.-atoms P per cubic metre corrected for salt error, it is necessary to multiply by $1{\cdot}35/71 = 0{\cdot}0190$.

To compare production of phytoplankton for different years, as deduced from phosphate records, Table III has been prepared to show the average content of the water column down to 20 m. (including the region of active photo-synthesis) and down to the bottom at 70 m. for every cruise to E 1 between March 1923 and August 1938. Furthermore, to establish whether

TABLE I. COMPLETE PHOSPHATE RECORDS AT STATION E 1 AUGUST 1930 TO AUGUST 1938; MG.-ATOM/M.^{3} P

All corrected for salt error.

Depth	1930					1931								
m.	12/8	10/9	9/10	11/11	4/12	13/1	4/2	19/2	23/3	7/4	22/4	18/5	10/7	26/8
0	0·10	0·00	0·33	0·50	0·53	0·53	0·58	0·46	0·25	0·42	0·23	0·11	0·07	0·03
5	0·06	0·00	...	...	...	...	...	...	0·21	0·28	0·17	0·11	0·07	0·04
10	0·05	0·05	...	...	...	...	...	...	0·26	0·24	0·18	0·14	0·08	0·08
15	...	0·18	...	...	...	...	...	...	...	...	0·20	...	0·09	0·04
20	0·13	0·18	...	...	...	...	...	...	...	...	...	...	0·12	...
25	0·24	0·20	0·27	0·51	0·48	0·48	0·49	0·49	0·25	0·25	0·19	0·13	0·15	0·04*
50	...	...	...	0·52	0·51	0·48	0·38	0·39	0·23	0·24	0·17	0·11	0·14	0·07
70†	0·23	0·20	0·33	0·48	0·60	0·49	0·40	0·47	0·26	0·25	0·16	0·10	0·17	0·07

Depth	1931					1932‡							1933	
m.	8/9	25/9	20/10	30/11	31/12	28/1	15/6	16/8	12/9	27/10	15/11	20/12	11/1	14/2
0	0·16	0·19	0·19	0·31	0·39	0·46	0·24	0·00	0·00	0·46	0·41	0·42	0·54	0·46
5	0·17	0·19	0·19	0·44	0·43	0·45	0·02	0·00	0·08	...	0·42	0·44	0·55	0·46
10	...	...	...	...	...	...	...	...	...	...	...	...	...	...
15	0·17	0·19	...	...	...	...	0·10	0·00	0·09	...	...	...	...	...
20	...	...	...	...	...	...	...	...	...	...	...	...	...	...
25	0·18	0·17	0·20	0·44	0·43	0·47	0·10	0·05	0·22	...	0·42	0·47	0·55	0·46
50	0·19	0·16	0·20	0·47	0·43	0·48	...	0·03	0·22	...	0·40	0·50	0·51	0·48
70†	0·26	0·20	0·18	0·45	0·43	0·46	0·24	...	0·28	...	0·42	0·57	0·51	0·48

Depth	1933									1934				
m.	13/3	4/4	11/5	18/7§	9/8	19/9	23/10	15/11	15/12	22/1	12/2	20/3	1/5	30/5‖
0	0·31	0·31	0·02	0·00	0·00	0·16	0·17	0·28	0·48	0·36	0·32	0·39	0·09	0·13
5	...	0·30	0·08	0·02	0·02	0·32	0·18	0·26	0·48	0·36	0·36	0·38	0·08	0·05
10	0·40	0·29	...	0·02	...	0·21	...	...	...	...	...	...	...	...
15	...	0·33	0·14	0·03	0·04	0·17	...	...	...	...	...	...	0·20	...
20	...	...	...	0·02	...	...	...	...	...	...	...	...	...	...
25	0·42	0·33	0·19	0·03	0·05	0·21	0·18	0·28	0·48	0·36	0·35	0·39	0·21	0·20
50	0·44	0·38	...	0·14	0·04	0·34	0·17	0·27	0·48	0·38	0·35	0·41	0·20	...
70†	0·48	0·35	0·22	0·15	0·06	0·33	0·23	0·27	0·48	0·38	0·35	0·39	0·21	0·20

Depth	1934						1935							
m.	9/7	15/8	21/9	18/10	14/11	20/12	15/1	26/2	22/3	2/5	4/7	8/8	16/10	21/11
0	0·00	0·00	0·09	0·21	0·23	0·35	0·41	0·44	0·54	...	0·07	0·02	0·20	0·43
5	0·03	0·00	0·09	0·21	0·26	0·33	0·41	0·44	0·39	0·11	0·06	0·03	...	...
10	...	...	...	...	...	...	...	...	...	...	...	...	...	...
15	0·14	0·00	...	...	...	...	...	...	...	...	0·07	0·12	0·25	0·41
20	...	...	...	...	...	...	...	...	...	...	...	...	...	...
25	0·13	0·19	0·10	0·22	0·24	0·33	0·43	0·42	0·42	0·24	0·13	0·15	0·25	0·41
50	0·16	0·19	0·24	0·19	0·24	0·33	0·42	0·42	0·37	0·25	0·23	0·16	0·25	0·41
70†	0·25	0·21	0·27	0·18	0·24	0·33	0·42	0·41	0·37	0·25	0·25	0·16	0·25	0·41

Depth	1935	1936							1937					
m.	13/12	23/1	10/3	28/4	12/5	18/6	22/7¶	30/9	14/1	18/2	19/5	17/6	22/7	21/9
0	0·45	0·58	0·24	0·10	0·29	0·07	0·06	0·13	0·48	0·47	0·05	0·03	0·05	0·10
5	0·45	0·44	0·22	0·10	0·05	0·01	0·06	0·14	0·49	0·48	0·00	0·04	0·05	0·10
10	...	...	...	...	...	...	0·07	...	...	...	...	...	...	...
15	...	0·46	0·22	0·13	0·18	0·05	...	...	...	...	0·06	0·05	0·06	0·10
20	...	...	...	...	...	...	...	...	...	...	...	...	...	...
25	0·46	0·47	0·31	0·19	0·22	0·10	0·24	0·25	0·47	0·49	0·10	0·22	0·30	0·13
50	0·46	0·47	0·41	0·24	0·27	0·26	0·24	0·34	0·49	0·49	0·26	0·28	0·33	0·26
70†	0·46	0·48	0·43	0·20	0·27	0·26	0·24	0·34	0·48	0·49	0·28	0·28	0·35	0·26

Depth	1937		1938								
m.	14/10	8/12	24/1	22/2	29/3	14/4	18/4	13/5	8/6	24/7	12/8
0	0·21	0·39	0·52	0·46	0·35	0·25	0·17	††	0·22	0·05	0·00
5	0·24	0·38	(0·66?)	0·46	0·30	0·26	0·15	0·22	0·06	0·04	0·00
10	...	...	...	...	...	...	...	...	...	0·06	...
15	0·21	...	...	0·46	...	0·26	...	0·19	0·09	0·04	0·01
20	...	...	...	...	...	...	...	0·19	...	0·09	...
25	0·21	0·38	0·45	0·49	0·41	0·28	0·17	0·29	0·11	0·12	0·04
50	0·21	0·39	0·45	0·48	0·42	0·32	0·18	0·24	0·20	0·26	0·18
70†	0·21	0·37	0·47	0·44	0·45	0·30	0·18	0·24	0·20	0·26	0·18

* 35 m., 0·04.
† Samples from 2–4 m. above the bottom.
‡ Interval February–May due to illness.
§ Station L 6.
‖ Station L 6, bottom sample at 55 m.
¶ Near E 1, 11 miles S.W. × W. of Eddystone.
†† See Table X.

any particular year was early or late, the maximum, minimum and average values that have been found for each of the twelve calendar months between March 1923 and February 1938 have been set out in Table IV. The differences between the averages for any two spring months gives the average monthly consumption at that time. It will be seen that by April, on an average, half of the year's supply of phosphate has been used up.

TABLE II. COMPLETE PHOSPHATE RECORDS AT STATION E 2, 1930 TO 1936. MG.-ATOM/M.^{3} P

All corrected for salt error.

Depth	1930	1931				1932	1933			1934				1935				1936
m.	9/10	4/2	22/4	26/8	30/11	15/11	14/2	9/8	13/11	12/2*	1/5	15/8	14/11	26/2*	2/5	4/7	21/11	12/5
0	0·42	0·42	0·58	0·01	0·27	0·50	0·36	0·00	0·52	0·52	0·22	0·00	0·25	0·39	...	0·00	0·37	0·11
5	...	...	0·34	0·02	0·38	0·50	0·36	0·00	0·53	...	0·27	0·00	0·27	0·40	0·32	0·02	...	0·10
10	...	...	0·33	0·04	...	...	...	...	...	...	...	...	...	...	...	...	...	...
15	...	...	0·29	0·04	...	...	...	0·00	...	...	0·27	0·00	...	...	...	...	0·37	0·12
25	...	0·40	0·30	0·05†	0·50	0·51	0·37	0·27	0·52	0·45	0·27	0·37	0·27	0·41	0·35	0·29	0·37	0·13
50	...	0·46	0·34	0·13	0·48	...	0·37	0·27	0·48	0·43	0·26	0·33	0·30	0·43	0·36	0·31	0·37	0·17
70–75	...	0·60	...	0·16	...	0·51	...	0·29	...	...	...	...	...	...	...	...	...	...
80–90	0·44	0·52	0·34	0·18	0·50	0·50	0·40	0·29	0·52	0·40	0·28	0·37	0·31	0·42	0·37	0·31	0·37	0·17

* Midway E 1–E 2; 33 miles S.W. of Eddystone. † 35 m., 0·05; 40 m., 0·07; 45 m., 0·13.

The consumption of phosphate as a measurement of plant production is affected by the length of time elapsing between two cruises. A more useful criterion of the intensity of an outburst is the consumption of phosphate per day (Fig. 1). Even here it should be recognized that the highest consumption may appear when cruises are very frequent (e.g. April 1938). Since a high intensity of production is unlikely to persist for a month or more, within that time a period of intense production may be partially masked by a preceding or following quiescent one. This comment applies with especial force in the years 1932 and 1937.

THE WINTER MAXIMUM OF PHOSPHATE

The maximum amount of phosphate is usually found at E 1 towards the end of December or beginning of January. This winter maximum is a measure of the amount of phosphate available for the following season's crop of phytoplankton and indirectly may control the survival of the larval planktonic stages of many marine animals.

Organically combined phosphorus, after allowing for the presence of arsenic, may amount to about 0·25 mg.-atom/m.^{3} (Cooper, 1937). There is evidence that organic phosphorus may become available fairly quickly (Cooper, 1935; Redfield, Smith & Ketchum, 1937; Seiwell & Seiwell, 1938). Since organic phosphorus is formed by the breakdown of living matter, at midwinter it is likely to be proportional to the inorganic phosphate available in a given area for plant growth. Deductions from records of the winter maximum of inorganic phosphate are therefore unlikely to be invalidated by vagaries of organic phosphorus.

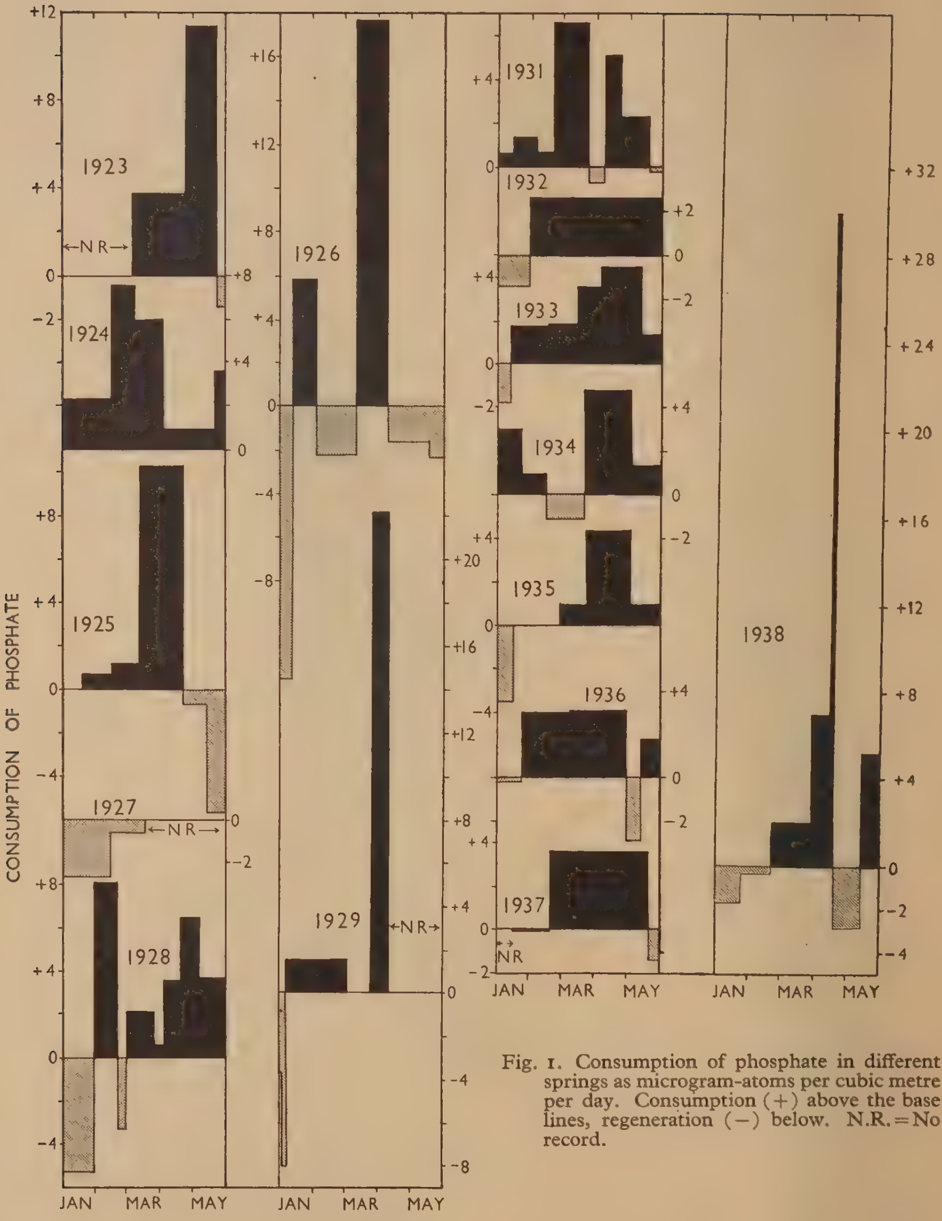


Fig. 1. Consumption of phosphate in different springs as microgram-atoms per cubic metre per day. Consumption (+) above the base lines, regeneration (−) below. N.R. = No record.

Table III. Average Phosphate Content between the Surface and 20 m. and between the Surface and Bottom at Station E 1

All corrected for salt error; mg.-atom/m.³ P.

	January			February			March			April			May			June		
	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.
1923	...	...	...	...	...	...	7	0·70	0·71	24	0·49	0·53	22	0·14	0·21	19	0·09	0·25
1924	2	0·73	0·715	15	0·615	0·615	10	0·37	0·44	4	0·28	0·29	20	0·19	0·25	17	0·08	0·17
1925	19	0·59	0·61	17	0·59	0·59	14	0·56	0·56	22	0·05	0·16	13	0·09	0·175	3	0·13	0·30
1926	12*	0·76	0·76	3	0·63	0·63	11†	0·68	0·71	10†	0·19	0·18	17†	0·21	0·24	24	0·18	0·33
1927	...	...	...	15	0·53	0·53	21	0·53	0·55	...	...	...	...	...	...	...	...	...
1928	31	0·71	0·69	21	0·52	0·52	1	0·55	0·55	5	0·47	0·49	7	0·26	0·325	4	0·175	0·210
							27	0·49	0·495	19	0·44	0·44				13	0·09	0·17
1929	2	0·68	0·66	...	...	...	4	0·61	0·61	11	0·24	0·27	...	...	...	...	...	...
	7	0·715	0·70				26	0·51	0·61									
1930	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1931	13	0·50	0·49	4	0·53	0·46	23	0·25	0·24	7	0·26	0·25	18	0·125	0·12	...	...	...
				19	0·475	0·45				22	0·19	0·18						
1932	28	0·46	0·47	...	...	...	...	...	...	...	...	...	...	...	...	15	0·09	0·135
1933	11	0·55	0·53	14	0·46	0·47	13	0·38	0·42	4	0·31	0·34	11	0·11	0·175	...	...	...
1934	22	0·36	0·37	12	0·35	0·35	20	0·385	0·39	...	...	...	1	0·14	0·19	...	...	...
1935	15	0·42	0·42	26	0·43	0·42	22	0·42	0·395	...	...	...	2	0·18	0·22	...	...	...
1936	23	0·47	0·47	...	...	...	10	0·23	0·23	28	0·12	0·18	12	0·15	0·22	18	0·04	0·155
1937	14	0·48	0·48	18	0·48	0·48	...	...	...	...	...	...	19	0·04	0·16	17	0·05	0·20
1938	24	0·48	0·46	22	0·46	0·47	29	0·34	0·40	14	0·26	0·29	13	c. 0·20	0·24	8	0·10	0·14
										18	0·16	0·17						

	July			August			September			October			November			December		
	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.	Day of month	0–20 m.	0–70 m.
1923	12	0·07	0·16	15	0·185	0·32	13	0·10	0·27	15	0·36	0·31	8	0·38	0·38	10	0·65	0·65
1924	9	0·09	0·19	7	0·06	0·20	3	0·28	0·34	1	0·25	0·28	12	0·37	0·38	9	0·615	0·615
1925	8	0·08	0·13	5	0·165	0·37	...	...	...	1	0·23	0·325	11	0·50	0·50	11	0·33	0·36
				31	0·05	0·09												
1926	8	0·115	0·20	16	0·03	0·195	22	0·06	0·16	19	0·35	0·35	24	0·495	0·49	14	0·52	0·54
																31	0·425	0·41
1927	...	...	...	...	...	...	...	...	...	...	...	...	4	0·38	0·44	9	0·59	0·59
1928	4	0·10	0·265	9	0·01	0·18	18	0·115	0·37	2	0·24	0·25	30	0·52	0·54	...	...	...
	11	0·06	0·27	16	0·12	0·23												
	23	0·03	0·20	29	0·20	0·30												
1929	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
1930	...	...	...	12	0·08	0·185	10	0·08	0·165	9	0·30	0·30	11	0·51	0·51	4	0·50	0·515
1931	10	0·075	0·13	26	0·05	0·06	8	0·17	0·19	20	0·195	0·195	30	0·43	0·445	31	0·425	0·43
							25	0·19	0·18									
1932	...	...	...	16	0·01	0·03	12	0·09	0·19	27	0·46	0·46	15	0·42	0·41	20	0·45	0·49
1933	18*	0·02	0·08	9	0·03	0·04	19	0·22	0·27	23	0·18	0·18	13	0·27	0·27	15	0·475	0·475
1934	9	0·08	0·14	15	0·00	0·14	21	0·09	0·18	18	0·21	0·20	14	0·25	0·24	20	0·33	0·33
1935	4	0·07	0·16	8	0·08	0·12	...	...	...	16	0·23	0·245	21	0·42	0·41	13	0·455	0·46
1936	22	0·09	0·20	...	...	...	30	0·17	0·27	...	...	...	...	...	...	...	...	...
1937	27	0·07	0·25	...	...	...	21	0·10	0·18	14	0·22	0·21	...	...	...	8	0·38	0·38
1938	24	0·05	0·17	12	0·02	0·09	...	...	...	...	...	...	...	...	...	...	...	...

* Station L 6. † All values in March, April and May 1926 may be high as the standard had deteriorated and the correction applied was only an approximation.

A fall in the winter maximum, from the level of earlier years of about 0·7 mg.-atom/m.^{3}, was noticed in 1930–1 and 1931–2. Since then it has remained within narrow limits—around 0·47 mg.-atom/m.^{3} (Table V).

The influx of warm saline Atlantic water into the English Channel in the autumn of 1921 and its marked effect on the climate of the south-west of England is well attested (Harvey, 1925). It is quite possible that this influx brought with it the relatively rich supply of nutrient salts which was found when the routine determinations of phosphate started in 1923. Atkins (1938) has suggested that the 1921 influx may be related to the remarkable maximum in the constant of solar radiation found by Abbot (1935) in the autumn of that year. Abbot has analysed his records of the solar constant and has found that the resulting periodicities, which are integral multiples or sub-multiples of 23 years, may be correlated with fluctuations in weather in different parts of the world. Such attempts to relate terrestrial weather to astronomical periodicities have occupied others, in particular, O. Pettersson (1914*a*, *b*). As to the shorter periods there is no general agreement but Pettersson has arrived at two long lunar periodicities of 92 and 111 years. Of these the first is an exact multiple of Abbot's 23-year period and the second is reasonably close to Abbot's period of $115 = 5 \times 23$ years. Since terrestrial weather appears to be the result of a large number of periodic astronomical functions closely interwoven, any speculative attempt to link up our results more closely with these would be premature. Meanwhile, it is essential that our routine determinations of phosphate shall be continued and that special attention be devoted to the autumn and winter of 1944–5 when a period of 23 years from the notable influx of 1921 will have elapsed.

Table IV. Average Phosphate Content of Water Column

Showing the maximum, minimum and "normal" or mean values found between March 1923 and February 1938 at the International Hydrographic Station E 1; mg.-atom/m.^{3} P, corrected for salt error.

Month	No. of years for which data are available	Average content between 0 and 20 m.			Average content of whole water column (70 m.)		
		Max.	Min.	Normal	Max.	Min.	Normal
Winter max.	13	..	..	...	0·76	0·42	0·559
January	13	0·76	0·36	0·554	0·76	0·37	0·548
February	11	0·63	0·35	0·506	0·63	0·35	0·503
March	12	0·70	0·23	0·465	0·71	0·24	0·490
April	9	0·49	0·05	0·262	0·53	0·16	0·292
May	11	0·26	0·04	0·149	0·32	0·12	0·208
June	8	0·18	0·04	0·100	0·33	0·135	0·216
July	11	0·115	0·02	0·075	0·27	0·08	0·171
August	11	0·20	0·00	0·068	0·37	0·03	0·160
September	11	0·28	0·06	0·126	0·37	0·16	0·235
October	12	0·46	0·18	0·269	0·46	0·18	0·275
November	12	0·52	0·25	0·412	0·54	0·24	0·418
December	12	0·65	0·33	0·473	0·65	0·33	0·481

Evidence in support of the view that the English Channel was enriched with phosphate during the 1921 influx of Atlantic water may be found in Matthews' pioneer phosphate determinations in 1916–17 (Matthews, 1917). His control experiments suggest that the method is free from salt error and the results appear to be accurate to within ±0·04 mg.-atom P/m.^{3} Due to war-time restrictions his samples were taken at the Knap Buoy which lies outside Plymouth Breakwater between stations L 2 and L 3. Admixture of estuarine water is liable to increase the amount of phosphate so that only waters having salinities greater than about 33·4 °/$_{oo}$ may be legitimately compared with station E 1. In 1916 on January 14, 18 and 24, he found respectively 0·45, 0·48 and 0·52 mg.-atom phosphate-P/m.^{3} In 1917 on January 10 the amount was somewhat higher, 0·62 mg.-atom P. In 1922, on February 12, when the winter maximum had almost certainly been passed, the Government Chemist using the same method found as much as 0·72 mg.-atom P (Atkins, 1923), agreeing closely with Atkins' own corrected analyses at that time and season. Our more recent records show that at midwinter, the phosphate content at stations L 2 and L 3, in waters more saline than 33·4 °/$_{oo}$, lies on an average about 0·05 mg.-atom P/m.^{3} higher than at E 1.

TABLE V. WINTER PHOSPHATE MAXIMA FOR WHOLE WATER COLUMN AT E 1

Calculated minimum production of phytoplankton and actual production of young fish.

					Minimum production of phytoplankton. Metric tons wet weight per sq. km. and depth of 72 m.		
Winter	Phosphate maximum, mg.-atom/m.^{3}	Deviation from mean, mg.-atom/m.^{3}	Percentage deviation from mean	Year	Between winter phosphate max. and May	Between winter phosphate max. and summer min.	Young fish summer spawners (Russell)
1921–22	>0·65*	>+0·09	>+16	1922	..	..	..
1922–23	>0·71†	>+0·15	>+27	1923	>1700	>1850	..
1923–24	0·71	+0·15	+27	1924	1600	1850	696
1924–25	0·61	+0·05	+9	1925	1500	1600	140
1925–26	0·76	+0·20	+36	1926	>1750	>2000	909
1926–27	0·55	−0·01	−2	1927	..	..	170
1927–28	0·69	+0·13	+23	1928	1250	1750	..
1928–29	0·69	+0·13	+23	1929	>1400	..	321
1929–30	..	..	..	1930	..	..	403
1930–31	0·52	−0·04	−7	1931	1450	1650	230
1931–32	0·47	−0·09	−16	1932	1150	1500	197
1932–33	0·53	−0·03	−5	1933	1200	1650	117
1933–34	0·48	−0·08	−14	1934	1000	1150	79
1934–35	0·42	−0·14	−25	1935	700	1000	37
1935–36	0·47	−0·09	−16	1936	800	1050	115
1936–37	0·48	−0·08	−14	1937	1100	1100	174
1937–38	0·47	−0·09	−16	1938	1050	1350	..
Mean 1923–24–1937–38	0·56	..	..	..	..	..	..

* March 1922 by Matthews' method.
† March 15 1923, 0·71 mg.-atom; maximum probably higher.

Although these investigations were the first to give even the right order of magnitude of the phosphate content of sea water, we may place considerable confidence in them. They suggest, firstly, that the phosphate content of the English Channel in 1916 and 1917 was similar to that in the 1930's and, secondly, that the increase took place between January 1917 and February 1922.

Table V shows also that in the winters of 1923–4 to 1928–9, the phosphate maximum averaged 0·67 mg.-atom/m.^{3}, whereas for the winters 1930–1 to 1937–8 it averaged only 0·48 mg.-atom. The high catches of young fish in the summer of 1930 suggest that the winter of 1929–30 was also one of high phosphate. The winter 1930–1 was therefore probably the first of low phosphate. Our results show a correlation with the direction of the residual current at the Varne lightship in the Straits of Dover (Carruthers, 1935). I am greatly indebted to Dr Carruthers for providing unpublished records required to bring the comparison up to date (Table VI). The records are arranged in order of decreasing easting of the current. In the four calendar years 1927–30 the average set of the current always lay between 25° and 40° east of north. In 1932–7, years of low phosphate, the average set lay between 8° west and 10° east of north. This comparison suggests that water of higher phosphate content is unlikely to work into the western end of the English Channel until the average residual current at the Varne lightship shows greater easting.

TABLE VI. COMPARISON BETWEEN WINTER PHOSPHATE MAXIMA AND REPRESENTATIVE DAILY WATER-FLOW PAST THE VARNE LIGHT VESSEL IN THE PRECEDING YEARS

Year Jan.–Dec.	Residual current at Varne; miles per lunar day towards a true direction	Winter	Phosphate maximum at E 1	
			mg.-atom/m.^{3}	Deviation from mean (%)
1927	3·1 N 40° E	1927–28	0·69	+33
1930	3·8 N 33° E	1930–31	0·52	0
1928	3·3 N 26° E	1928–29	0·69	+33
1929	3·2 N 25° E	1929–30	..	..
1931	3·2 N 18° E	1931–32	0·47	−10
1935	4·2 N 10° E	1935–36	0·47	−12
1936	4·1 N 9° E	1936–37	0·48	− 8
1934	3·9 N 7° E	1934–35	0·42	−19
1932	3·5 N 6° E	1932–33	0·53	+ 2
1937	3·5 N 6° E	1937–38	0·47	−10
1933	2·9 N 8° W	1933–34	0·48	− 8
		Mean*	0·52	..

* Mean of winters 1927–8–1937–8, except 1929–30 for which no records are available. This mean is not the same as that in Table V.

THE RELATION BETWEEN THE WINTER PHOSPHATE MAXIMA AND ABUNDANCE AND COMPOSITION OF PLANKTON AND YOUNG FISH

Russell (1935, 1936) has found that fluctuations in the phosphate content at E 1 are closely correlated with fluctuations in numbers and changes in composition of the plankton population. Broadly speaking water poor in phosphate as judged by the winter maximum, is characterized by the presence of *Sagitta setosa*, scarcity of all other holoplanktonic organisms, and poor production of the young of summer spawning fish. Water rich in phosphate is associated with *S. elegans* and other indicators of "Atlantic" water, a rich and varied zooplankton population and successful production of young fish. For a more detailed account of this topic Russell's papers must be consulted.

In any study of the impoverished state of the fisheries in the western end of the English Channel, the question of overfishing must take pride of place. If the intensity of fishing exceeds the natural recovery rate of the stock, the chemical and biological conditions governing that recovery rate are of lesser importance. Even so the evidence is growing ever stronger that the impoverishment, at least in part, may work back to the depletion of inorganic phosphate available in the first place for the growth of phytoplankton and ultimately for that of all animals living in our waters. As yet we are unable to say whether the richer conditions of the 1920's or the poorer ones of the 1930's are the more normal or whether both form part of some cyclical process which will recur. Even so it would appear that any considerable improvement in the fisheries is likely to be preceded, not only by a lesser intensity of fishing, but by an increase in the available inorganic phosphate and with predominance of *Sagitta elegans* over *S. setosa* in the western end of the Channel.

More detailed Comparison of the Years 1923 to 1937

The interval between the time of the winter maximum for phosphate and mid-May (Table III) covers the vernal outburst of diatoms and the consumption of phosphate is an index of the quantity of phytoplankton produced. The years may be grouped in order of productivity:

★★★★★	1923	1926		
★★★★	1924	1925	1929	1931
★★★	1928	1933		
★★	1932	1934	1937	1938
★	1935	1936		

In several of the earlier years much of the phosphate was used up in short periods of intensive plant production. Nevertheless 1932, 1934, 1937 and 1938 were probably poor survival years and 1935 and 1936 must have been exceptionally bad. In 1935 not only was the winter maximum the lowest on record but of this phosphate only 49 % was used between January and May, the lowest percentage utilization yet recorded. The entire consumption during these five months was considerably less than during several periods of a few weeks in earlier years. These conditions were mirrored in the exceedingly low production of young fish in that year, also the lowest recorded (see Table V).

Due no doubt to different degrees of vertical mixing in different years (cf. Atkins, 1930, p. 825), the percentage consumption of the total inorganic phosphate content of the water column fluctuates between 49 and 81 % for the spring period and between 63 and 93 % for the period between winter maximum and summer minimum. Although some phosphate may be regenerated and used more than once in one growing season, these fluctuations are probably highly significant. For example although the maximum in the winter 1930–1 was only 0·52 mg.-atom/m.^{3}, the efficiency of phosphate utilization in the following spring and early summer was so high that the year 1931 is placed in the "four star" class in the list on p. 189. If other periods be studied in Table III similar variations will be found between the different years which may be of significance for the survival of young fish.

In 1931 (Cooper, 1933*b*) calculations of minimum crop production were made on the basis of the fall in several nutrient salts between the winter maximum and summer minimum at station E 1 (Table VII). The figure for phosphorus has now been corrected for salt error. The oxygen calculation is almost certainly too low and the nitrate-nitrogen took no account of other available forms of nitrogen such as ammonia. Such a calculation based on total inorganic nitrogen has been added to Table VII. Even this is rather uncertain since we know nothing of the amounts of urea, amino-acids and other simple organic nitrogen compounds which may quickly become available. The agreement is good and a figure of about 1650 metric tons for a water column one sq. kilometre in area and 72 m. deep seems representative. This was associated with a consumption of 0·46 mg.-atom P/m.^{3} (corrected). On this basis crop figures have been calculated for all the years for which data are available (Table V). A summarized account of phytoplankton production follows:

TABLE VII

1931 Between	On basis of change in	Phytoplankton produced, wet weight. Metric tons per sq. km. of surface for a depth of 72 m.
4/12 and 26/8	Phosphorus	1650
19/2 and 10/7	CO_2	1730
23/3 and 10/7	Nitrate-N (incl. nitrite-N)	1270
23/3 and 18/5	Total inorganic N	1350
19/2 and 26/8	O_2 lost to atmosphere	1000

PRODUCTION OF PHYTOPLANKTON 1923–38, AS DEDUCED SOLELY FROM NUTRIENT SALT DATA

(In this account "available phosphate" means the winter maximum available for the following year's production.)

1923 No data until March 7. Probably little production until then. Average consumption of phosphate during April. Very heavy consumption during May. A late year.

1924 Production started in January and continued steadily until June. Although definitely an early year, conditions were good throughout for the survival of young fish dependent on phytoplankton. The water was, however, very cold.

1925 Production was crowded into the 6 weeks between March 14 and April 22 when two-thirds of the available phosphate and also silica were consumed. Possibly a poor survival year for all organisms other than those able to use this concentrated production of diatoms. Much of this may have gone to waste.

1926 Three-quarters of the available phosphorus was used in the four weeks, March 11–April 10. In this period the consumption was greater than the total amounts available for use in the springs of 1932, 1934, 1935, 1936, 1937 and 1938 and equal to those of 1931 and 1933.

1927 A very late year. Regeneration of phosphate preponderated up to March 21 after which no phosphate data are available. Nitrate results show considerable production in April and May.

1928 "Early and late." Periods of strong production: January 31–February 21; March 27–April 5; April 19–May 5. The first two were periods of diatom production, the last one of *Phaeocystis* or other non-siliceous phytoplankton. The period February 21–March 27 was one of regeneration and conditions were then unfavourable.

1929 On the whole an average year. Although some production occurred between January 7 and March 4, the vernal outburst cannot be said to have got under way before March 26. In the fortnight following, one half of the available phosphate was consumed. Records cease on April 11. Such intense short period production as occurred in 1925, 1926 and 1929 is not likely to be of great value to the herbivores since these are thought to avoid dense growths of phytoplankton.

1930 No records.

1931 An early year. Production started in December and was well spread out. The month February 19–March 23 was the peak period during which 40 % of the available phosphate was used.

1932 Inadequate data.

1933 A late year but even so has much in common with 1931.

1934 "Early and late." Greatest production occurred in January and April. February and March were poor months.

1935 Very late and exceptionally poor. April was the only month with production of any consequence, consumption of phosphate being then about average. Not only was the initial stock of phosphate very low, but it was very inadequately used.

1936 A poor year. Some consumption of phosphate occurred throughout February, March and April.

1937 In mid-February no sign of any vernal outburst was apparent. No further records are available until mid-May when surface phosphate was nearly exhausted.

1938 A late year and poor; 25 % of the total phosphate was used up in four days, April 14–18, and 50 % during the first three weeks of April. This represented four-fifths of the spring minimum production.

N.B. All the years after 1930 are affected by the marked fall in the winter maximum for phosphate which took place about then.

Autumn Diatom Outbursts

In the late summer and autumn the chemical evidence is difficult to interpret owing to the uncertain balance between consumption by plants and regeneration from dead material. The evidence suggests that outbursts occurred as follows:

1923	August, September.
1924	September.
1925	August.
1926	None.
1927	(No records.)
1928	September (1st fortnight).
1929	(No records.)
1930	None.
1931	August?
1932	None.
1933	End September–mid-October.
1934	None.
1935	?
1936	?
1937	August?

THE SPRING OUTBURSTS AT STATIONS E 1 AND E 2

Attention has been drawn (Atkins, 1930; Cooper, 1933*a*) to the quite different behaviour of the water masses at these stations between the February and May cruises. Three further years' work has added more data which repay examination (Tables VIII and IX). In only one year has more phosphate been found in February at E 2 than at E 1 and in five out of nine years the amount has been much less. Either the spring outburst regularly starts earlier in the more southerly waters, or, equally regularly, Station E 2 is occupied by a body of water quite different from that at E 1. The salinities shed no light on this. However, when the February results are examined in conjunction with the next cruise in May, it is seen that for every year except 1934 production at E 1 has far outstripped that at E 2 (Table IX). For the nine years for which we have phosphate records, the mean production in the upper layers at E 1 was twice as great as that at E 2. It is difficult to allow for the different depths at the two stations but, if the calculations are based on the changes in the whole water column to the bottom, the same general picture emerges. There is probably

TABLE VIII. AVERAGE CONTENT OF WATER COLUMN BETWEEN THE SURFACE AND 20 M. DEPTH AT STATIONS E 1 AND E 2 IN FEBRUARY; MG.-ATOM/M.^{3} P

Date	E 1	E 2
4/2/31	0·53	0·41
12/2/34	0·35	0·48*
14/2/33	0·46	0·365
15/2/27	0·53	0·51
15/2/24	0·615	0·59
17/2/25	0·59	0·37
21/2/28	0·52	0·42
26/2/35	0·43	0·40*
Mean	0·50	0·44
Also 11/3/26	0·68	0·47

* Station midway E 1–E 2.

TABLE IX. FALL IN THE AVERAGE PHOSPHATE CONTENT OF THE WATER COLUMN BETWEEN THE SURFACE AND 20 M. DEPTH AT STATIONS E 1 AND E 2 BETWEEN THE FEBRUARY AND MAY CRUISES; MG.-ATOM/M.^{3} P

Year	Between cruises of	Fall at E 1	Fall at E 2
1929	Jan. 7–Mar. 26	0·20	0·17
1931	Feb. 4–Apr. 22	0·34	0·06
1934	Feb. 12–May 1	0·21	0·21
1924	Feb. 15–May 20	0·42	0·32
1925	Feb. 17–May 13	0·50	0·18
1928	Feb. 21–May 7	0·26	0·20
1935	Feb. 26–May 2	0·25	0·07
1923	Mar. 7–14–May 22–25	0·56	0·28
1926	Mar. 11–May 17	0·47	0·05
	Mean for nine years	0·36	0·17

more vertical mixing of the water in mid-Channel, but while this may tend to keep down multiplication of the diatoms in stormy weather, it should also help to bring up the bottom store of phosphate into the optimum photosynthetic zone. Cruises to E 2 were discontinued in 1936.

Surface Regeneration of Phosphate

Atkins (1930) found large quantities of phosphate, up to 3 mg.-atom/m.^{3}, at the L series of stations on January 2 1929 and attributed them to regeneration of phosphorus from organic material at the surface. Supporting evidence for this view is set out in Table X which includes all occasions when the phosphate content of the surface water was at least 0·1 mg.-atom/m.^{3} greater than at 5 m.

Table X. Surface Regeneration of Phosphate at Station E 1

Depth (m.)	2/1/29	23/1/36	31/1/28	1/3/28	21/3/27	22/3/34	7/4/31	12/5/36	13/5/38
0	0·91	0·58	0·82	0·63	0·78	0·54	0·42	0·58	*
5	0·64	0·44	0·67	0·49	0·51	0·39	0·28	0·44	0·22
Average 5–25	0·64	0·46	0·68	0·53	0·52	0·41	0·25	0·46	0·22

Depth (m.)	8/6/38	15/6/32	4/7/28	11/7/28	16/8/28	29/8/28	23/9/26	19/10/26	24/11/26
0	0·22	0·24	0·23	0·16	0·65	0·46	0·29	0·49	0·78
5	0·06	0·02	0·09	0·03	0·02	0·07	0·10	0·32	0·46
Average 5–25	0·09	0·06	0·08	0·05	0·10	0·21	0·09	0·32	0·48

* Triplicate analyses on three samples taken in one routine haul, 1·10, 1·10, 1·13; analysis on sample collected half an hour later, 0·44.

Occasionally, as in the four cruises in June and July, this might be attributed to the light at the surface being too intense for active photosynthesis, depletion of phosphate occurring at the optimum depth around 5 or 10 m. This explanation cannot hold at other seasons. On May 13 1938, analyses showed a large change in surface phosphate whilst the ship was drifting freely at Station E 1. Since this type of irregularity is confined to surface samples, contamination only of these is highly unlikely. The phenomenon is not confined to any one season of the year and appears to be independent of weather conditions. High surface phosphate values have been found following calm and stormy weather and with winds from all points of the compass. It is true that winds from the southerly and westerly quadrants have predominated, but these are the prevailing winds of the district. Regeneration of phosphate from decomposing floating organic material, as suggested by Atkins, provides the only reasonable explanation.

I am indebted to Dr H. W. Harvey for collecting the greater part of the water samples used in this work, also to Mr C. F. Hickling and Mr P. G. Corbin for some in 1937 and 1938.

Summary

At Station E 1, 22 sea miles south-west from Plymouth, the winter maximum for phosphate, representing the stock available for plant growth in the following spring, averaged 0·67 mg.-atom/$m.^3$ for the winters 1923–4 to 1928–9 and only 0·47 mg.-atom for 1930–1 to 1937–8. This fall in phosphate shows a close correlation with the abundance of summer-spawning young fish (Russell). Since water containing similar low phosphate appeared to occupy the English Channel in 1916 (Matthews), the inflow of warm Atlantic water in the autumn of 1921 may well have brought with it the relatively rich phosphate found in the 1920's.

The impoverishment of phosphate around 1930 runs parallel with a decrease in the easting of the residual current at the Varne lightship in the Straits of Dover (Carruthers).

On the basis of spring phosphate consumption, the years may be classified in order of productivity:

★★★★★	1923	1926		
★★★★	1924	1925	1929	1931
★★★	1928	1933		
★★	1932	1934	1937	1938
★	1935	1936		

The efficiency of utilization of the total stock of phosphate varies from year to year. In 1935 it was only 63 % whereas a much higher percentage, 93 %, placed 1931 in the four star class.

Between February and May, the phosphate consumption in the upper layers at E 1, averaged over nine years, is twice as great as that at E 2 in mid-Channel.

REFERENCES

Abbot, C. G., 1935. Solar radiation and weather studies. *Smithsonian Misc. Coll.*, Vol. 94, No. 10, pp. 1–89.

Atkins, W. R. G., 1923, 1925, 1926, 1928, and 1930. Seasonal changes in the phosphate content of sea water in relation to the growth of the algal plankton. *Journ. Mar. Biol. Assoc.*, Vol. xiii, pp. 119–50, 700–20; Vol. xiv, pp. 447–67; Vol. xv, pp. 191–205; Vol. xvi, pp. 821–52.

— 1938. British fisheries, phosphate and the solar radiation constant. *Nature*, Vol. 141, p. 77.

Carruthers, J. N., 1935. The flow of water through the Straits of Dover. Part II. *Fishery Investigations*, Ser. ii, Vol. xiv, No. 4, pp. 1–67.

Carter, N. M., Moberg, E. G., Skogsberg, T. & Thompson, T. G., 1933. The reporting of data in oceanographical chemistry. *Proc. Fifth Pacific Sci. Congress.* Victoria and Vancouver, B.C., Vol. 3, pp. 2123–7.

Cooper, L. H. N., 1933*a*, *b* and *c*. Chemical constituents of biological importance in the English Channel. Parts I, II and III. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 677–728, 729–54; Vol. xix, pp. 55–62.

— 1933*d*. A system of rational units for reporting nutrient salts in sea water. *Journ. Cons. Int. Expl. Mer*, Vol. viii, pp. 331–4.

Cooper, L. H. N., 1935. The rate of liberation of phosphate in sea water by the breakdown of plankton organisms. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 197–202.

— 1937. "Organic" phosphorus in sea water from the English Channel. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 673–8.

— 1938. Salt error in determinations of phosphate in sea water. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 171–8.

Harvey, H. W., 1925. Evaporation and temperature changes in the English Channel. *Journ. Mar. Biol. Assoc.*, Vol. xiii, pp. 678–92.

— 1928. Nitrate in the Sea. Parts I and II. *Journ. Mar. Biol. Assoc.*, Vol. xiv, pp. 71–88; Vol. xv, pp. 183–90.

— 1934. Annual variation of planktonic vegetation, 1933. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 775–92.

Harvey, H. W., Cooper, L. H. N., Lebour, M. V. & Russell, F. S., 1935. Plankton production and its control. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 407–42.

Matthews, D. J., 1917. On the amount of phosphoric acid in the sea water of Plymouth Sound. I and II. *Journ. Mar. Biol. Assoc.*, Vol. xi, pp. 122–30; 251–7.

Pettersson, O., 1914*a*. Studien in der Geophysik und der kosmischen Physik. *Ann. d. Hydr. usw., Jahrg.* 42, pp. 141–6, 209–19, 255–70.

— 1914*b*. On the occurrence of lunar periods in solar activity and the climate of the earth. *Ur Svensk Hydrogr.-Biol. Komm. Skr.*, Vol. v, Eighth paper, pp. 1–20. (Also other papers in this journal including new series.)

Redfield, A. C., Smith, H. P. & Ketchum, B., 1937. The cycle of organic phosphorus in the Gulf of Maine. *Biol. Bull.*, Vol. lxxiii, pp. 420–43.

Russell, F. S., 1935. The seasonal abundance and distribution of the pelagic young of teleostean fishes caught in the ring trawl in off-shore waters in the Plymouth area. Part II. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 147–80.

— 1936. The importance of certain plankton animals as indicators of water movements in the western end of the English Channel. *Rapp. Proc.-Verb. Cons. Int. Expl. Mer*, Vol. c, pp. 7–10.

Seiwell, H. R. & Seiwell, G. E., 1938. The sinking of decomposing plankton in sea water and its relationship to oxygen consumption and phosphorus liberation. *Proc. Amer. Phil. Soc.*, Vol. 78, pp. 465–81.

THE DISTRIBUTION OF PHOSPHATES IN THE SOUTH-WESTERN AREA IN APRIL 1938

By C. F. Hickling, M.A.

Fisheries Laboratory, Lowestoft

(Text-fig. 1)

In April 1938 the Ministry of Agriculture and Fisheries research-vessel, *George Bligh*, surveyed, in connexion with a programme of mackerel research, a large area of sea in the western English Channel, St George's Channel, and to the west of Cornwall. The opportunity was taken of estimating the distribution of the phosphate in this area by means of the "Lowestoft Photometer". This instrument has been described by Graham (1936). In preparing the samples for use in the photometer, 3 c.c. of molybdate reagent were added to about 140 c.c. of the sample to be tested, and 4–6 drops of $SnCl_2$ solution.

In the first four charts in Fig. 1 are given the values of phosphate found at each station, at four depths, namely, at the surface, at 25, and 50 m., and at the bottom. The values are expressed as mg. P_2O_5 per cu. m., and have been raised by the factor 1·3 to allow for salt error. Contours have been inserted in the charts as follows: a hatched contour to include values greater than 50, a stippled contour to include values of from 40–50, and a contour to include values of 30–40 mg. per $m.^3$

No high degree of accuracy is claimed for these observations, for, as Graham points out, at high concentrations of phosphate the instrument is less reliable than at low concentrations; further, certain stations have been rejected because the instrument appeared to be faulty. There is, however, some internal evidence that the determinations are at least consistent, for when the itinerary of the ship brought her back into regions visited shortly before, the phosphate values were found to be in good agreement with those found previously.

The season in which the cruise was made was unfavourable for a survey of the distribution of the phosphates, for Cooper (1938) shows that, on an average, the consumption of phosphate by the phytoplankton has so far advanced, by April, that about half the year's supply has been used up. Nevertheless, in view of the scarcity of observations on the distribution of phosphates in the south-western area, it has been thought worth while to present the results obtained.

The charts show that, generally speaking, there was much more phosphate in the deeper water than at the surface. At the sea bottom, values greater than 30 mg. per cu. m. were found almost everywhere, whereas, at the surface, they

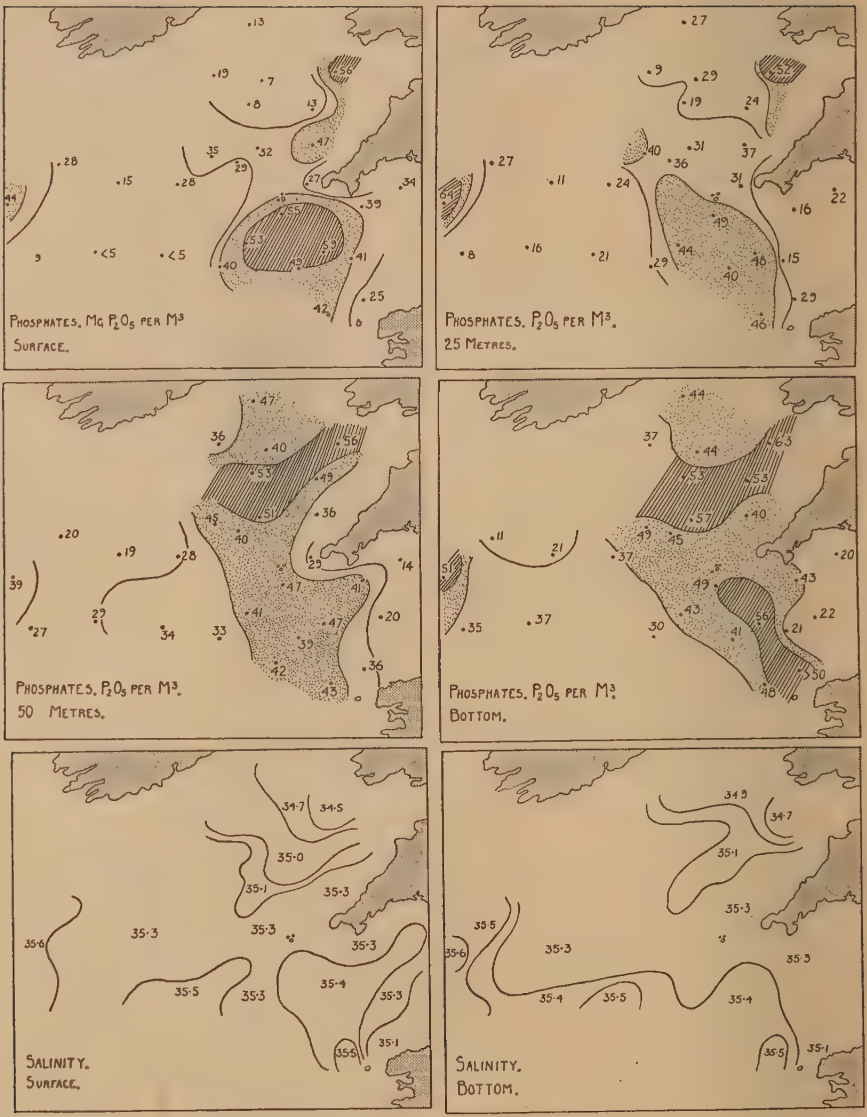

PHOSPHATES. MG P₂O₅ PER M³
SURFACE.
PHOSPHATES. P₂O₅ PER M³.
25 METRES.
PHOSPHATES. P₂O₅ PER M³.
50 METRES.
PHOSPHATES. P₂O₅ PER M³.
BOTTOM.
SALINITY.
SURFACE.
SALINITY.
BOTTOM.

Fig. 1. Distribution of phosphate in the south-western area in April 1938, with salinities at surface and bottom.

were restricted. But at all depths there were three regions where phosphate was especially abundant, namely, off the Bristol Channel, off the English Channel, and on the edge of the Continental Shelf west of Cornwall.

Variations in the distribution of phosphate in the sea are, of course, due not only to water movements, which may carry water rich in phosphate into regions poorer in phosphate, but also to the consumption and regeneration of phosphate *in situ* by living organisms. The first factor named may perhaps be traced, in the present data, by a comparison with the salinity of the water. In Fig. 1, in addition to the four charts of phosphate distribution, are given two charts showing the salinity at the surface and at the bottom.

A tongue of water of low salinity appeared to spread westwards from the Bristol Channel, and this tongue of low salinity is closely associated with the area rich in phosphate lying off the Bristol Channel. It may be that this phosphate-rich water was derived from the extensive watershed draining into the Bristol Channel. Kalle (1937) showed that the sea in the neighbourhood of the great rivers draining into the North Sea was rich in phosphate, and Graham (1938) shows that an area rich in phosphate may be associated with the drainage from the Thames, including, of course, the output of phosphates from the London sewage.

More saline water appeared to spread from the south across and into the English Channel, and also to be present on the edge of the Continental Shelf. Probably this more oceanic water carried with it a richer supply of phosphate, derived from the upwelling of deeper water, and would in part account for the areas richer in phosphate lying at the mouth of the English Channel, and at the edge of the Continental Shelf.

As to the biological factors affecting the distribution of the phosphate, these may be seen in the scarcity of phosphate in the surface water, as compared with the deeper water. Further, stations in certain regions were markedly rich in phytoplankton. This was, in many cases, shown by the colour and smell of the water, as well as by the observed presence of the larger diatoms in the reagent tubes. Through the kindness of Mr Corbin I have had a list of the stations at which phytoplankton was plentiful in the plankton catches; and it is clear that the area comparatively poor in phosphates, which lay between the richer areas off the English Channel and at the edge of the Continental Shelf, was an area in which the phytoplankton was developing rapidly.

SUMMARY

The results of a survey of the distribution of phosphates in the south-western area in April 1938 show that there were three regions exceptionally rich in phosphate. These regions appeared to be associated respectively with the outflow of the Bristol Channel, with the flow of more oceanic water across the entrance of the English Channel, and with upwelling of deeper water at the edge of the Continental Shelf.

The surface water was poorer in phosphate than the deeper water, and regions poorer in phosphate were in some cases associated with a crop of phytoplankton.

REFERENCES

COOPER, L. H. N., 1938. Phosphate in the English Channel, 1933–8, with a comparison with earlier years, 1916 and 1923–32. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 181–95.

GRAHAM, M., 1936. The Lowestoft Photometer. *Jour. du Conseil*, Vol. XI, No. 2.

GRAHAM, M., 1938. Phytoplankton and the Herring. Part III. Distribution of Phosphate in 1934–1936. *Min. Agric. Fish., Fish. Invest.*, Ser. II, Vol. XVI, No. 3, pp. 1–26. See also Graham and Harding, this Journal, pp. 201–6.

KALLE, K., 1937. Nahrstoff-untersuchungen als hydrographisches Hilfsmittel usw. *Ann. d. Hydr. usw.* LXV. Jahrg. H1, Berlin, 1937.

SOME OBSERVATIONS OF THE HYDROLOGY AND PLANKTON OF THE NORTH SEA AND ENGLISH CHANNEL

By Michael Graham, M.A., and J. P. Harding, Ph.D.

Fisheries Laboratory, Lowestoft

(Text-figs. 1–4)

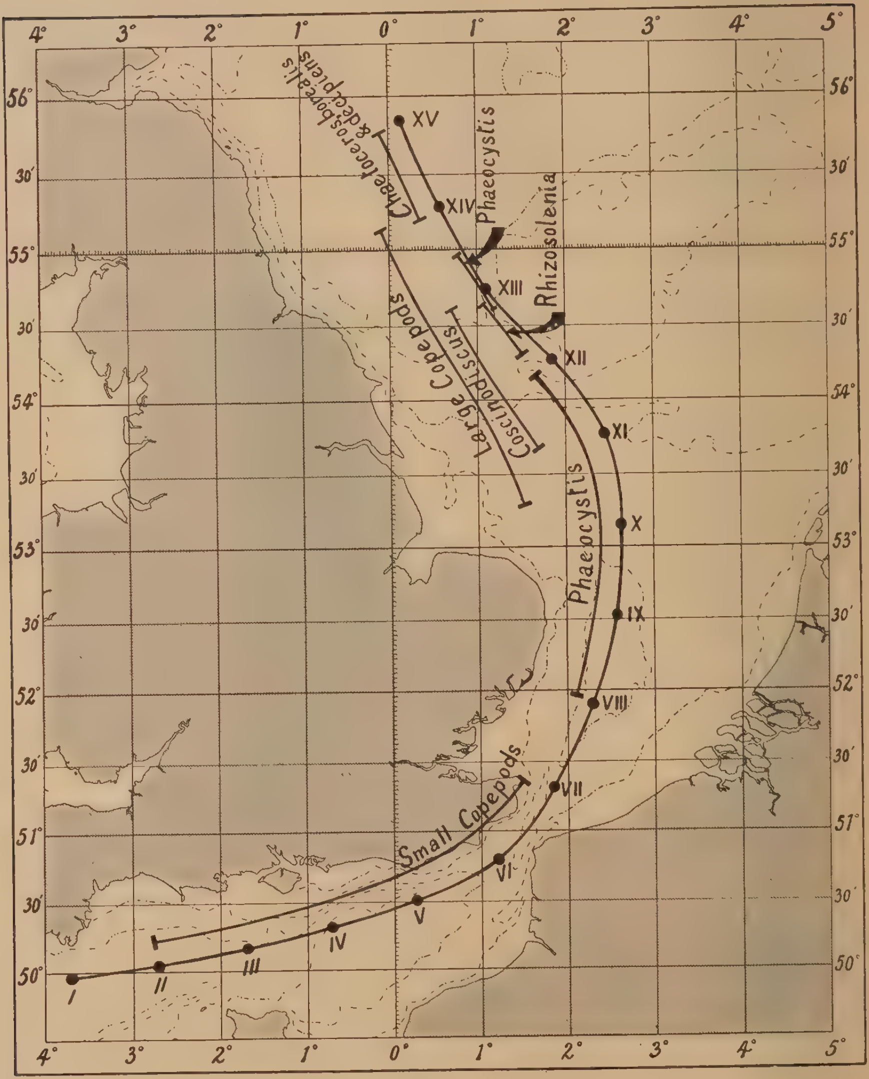
In April 1935 a vacant period in the programme of the research vessel *George Bligh* was occupied in determining the phosphate content of the waters of a selected line of stations in the North Sea and English Channel. The object was to extend the usual observations of phosphate in the North Sea, which form the subject of a separate paper (Graham, 1938), in the directions from which the southern North Sea receives its more oceanic water. It was thought in particular that observations between the southern North Sea and the area regularly examined from the laboratory at Plymouth would have an intrinsic interest. The distribution of the phosphate found in 1935 seemed to be of sufficient interest to warrant repetition of the experiment in 1936 and again in 1937.

Observations were made along the line drawn on the chart (Fig. 1). The positions marked I–XV on this chart correspond to the vertical lines I–XV in Figs. 2–4. The stations at which the observations were actually made lie near this line in positions indicated by circles in Figs. 2–4. The exact positions have been published in the *Bulletin Hydrographique* of the International Council for the cruises of the *George Bligh* April 26–30 1935, and May 13–18 1936, and will be published for the cruise April 8–15 1937.

Temperature, salinity and phosphate determinations were recorded at 10 m. intervals from surface to near bottom at each station, and samples of the plankton were taken with Hensen's net.

The phosphate content was determined in 1935 by the Atkins-Denigés method, as recommended by the conference which met in Oslo in 1928, recorded in the *Rapports et Procés-Verbaux des Réunions du Conseil International*, Vol. LIII, pp. 96–100. In 1936 and 1937 the phosphate was determined with the "Lowestoft Photometer" (Graham, 1936).

The season at which it was possible to do this work was not particularly suitable because the phosphate content of the water was changing rapidly near the spring outburst of diatoms. Nevertheless, certain features have been repeated. There is a tendency for areas of high phosphate content to be associated with extremes of salinity and temperature, and three sources of phosphate are recognized: (i) A trough of cool deep water connecting the



4°
3°
2°
1°
0°
1°
2°
3°
4°
5°
56°
30′
55°
30′
54°
30′
53°
30′
52°
30′
51°
30′
50°
Chaetoceros borealis & decipiens
Phaeocystis
Rhizosolenia
Large Copepods
Coscinodiscus
Phaeocystis
Small Copepods
XV
XIV
XIII
XII
XI
X
IX
VIII
VII
VI
V
IV
III
II
I

Fig. 1.

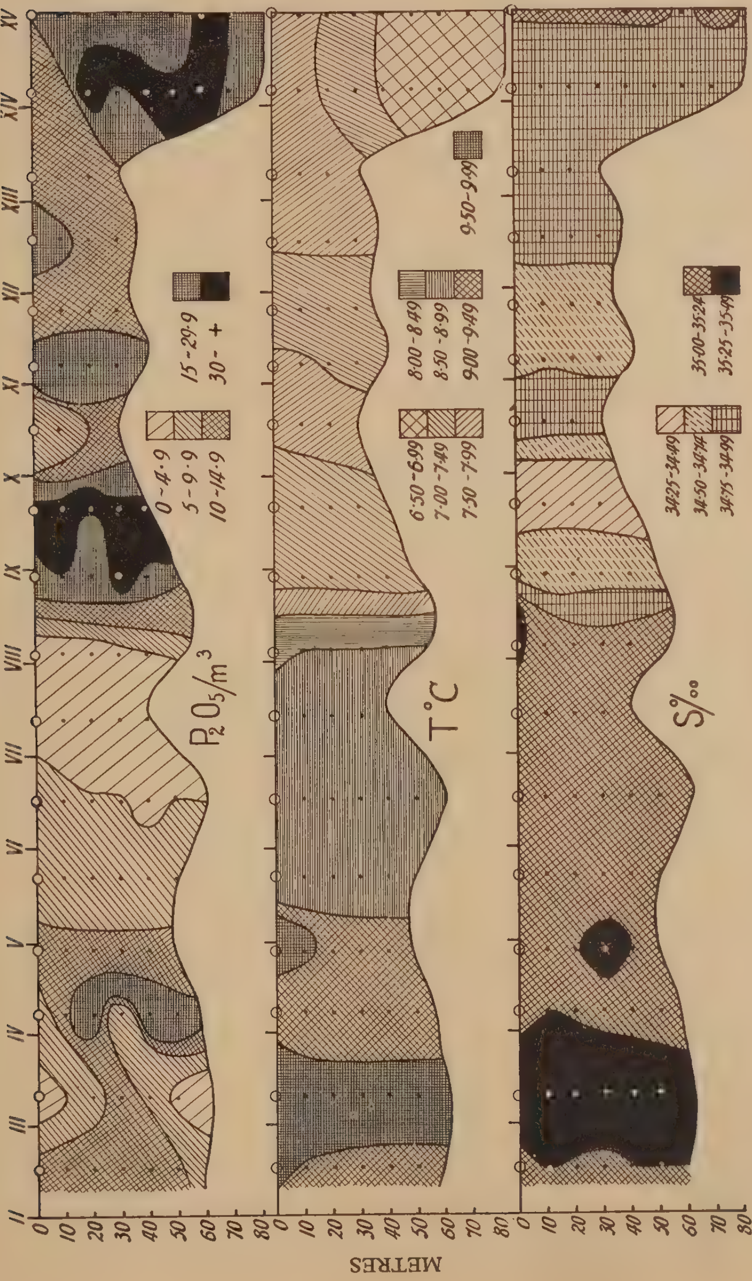

II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
XIV
XV
0
10
20
30
40
50
60
70
80
METRES
P_2O_5/m^3
0-4·9
5-9·9
10-14·9
15-29·9
30- +
T°C
6·50-6·99
7·00-7·49
7·50-7·99
8·00-8·49
8·50-8·99
9·00-9·49
9·50-9·99
S‰
34·25-34·49
34·50-34·74
34·75-34·99
35·00-35·24
35·25-35·49

Fig. 2. 1935.

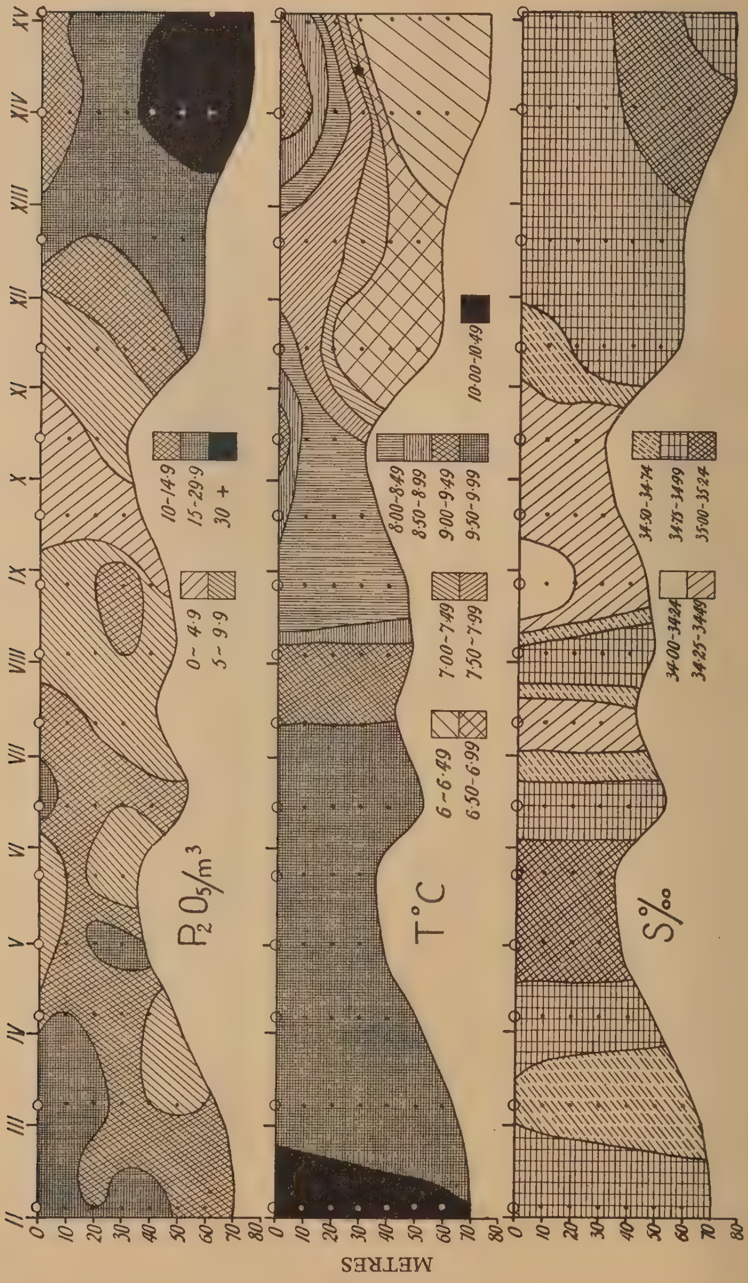

II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
XIV
XV
0
10
20
30
40
50
60
70
80
METRES
P_2O_5/m^3
0 - 4·9
5 - 9·9
10-14·9
15-29·9
30 +
T°C
6-6·49
6·50-6·99
7·00-7·49
7·50-7·99
8·00-8·49
8·50-8·99
9·00-9·49
9·50-9·99
10·00-10·49
S‰
34·00-34·24
34·25-34·49
34·50-34·74
34·75-34·99
35·00-35·24

Fig. 3. 1936.

southern North Sea with the more oceanic water of the northern North Sea, which was found to have a high phosphate content; (ii) Irregular areas of high phosphate content in the warmer Channel waters, which may be assumed to be oceanic in origin; and (iii) An area of low salinity about position IX, which was found to have a high phosphate content. This area was most pronounced in April 1935 and April 1937, and there was some indication of it in May 1936. The water here tended to be a little cooler than the surrounding water. The interpretation of these features is helped by the observations of other cruises. The high phosphate content of the northern part is ascribed to accumulation of phosphate under the thermocline, indications of which are present even at this early season. In the same way the high phosphate associated with low salinity in part of the southern North Sea is recognized as similar to areas of high phosphate found in other cruises and ascribed to the sewage of the River Thames. In regard to the Channel, the records from Plymouth for the International hydrographic station E 1 (Atkins, 1930; Cooper, 1933; and Harvey *et al.* 1935, and more recent records from the *Bulletin Hydrographique*) show that the phosphate near the bottom of this part of the Channel is rarely less than 10 mg. $P_2O_5/m.^3$ This condition is found to extend up the Channel but is lost near the Straits of Dover, where the water tends to

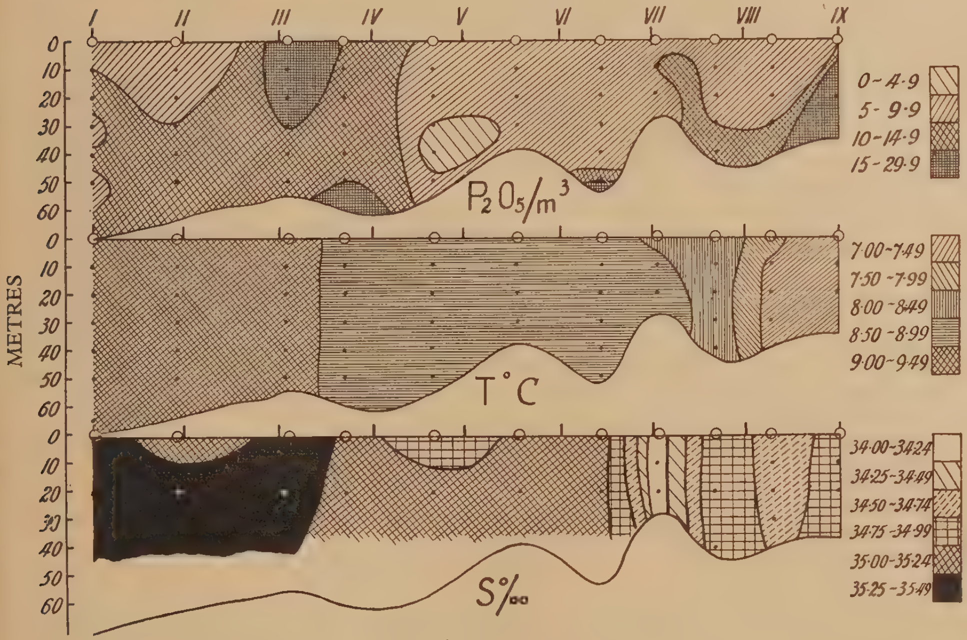


Fig. 4. 1937.

have very low concentration. There is no obvious explanation of why phosphate in the Channel does not reach the North Sea.

In regard to the larger plankton organisms that are taken in Hensen's net, the main features were also repeated in all three years. The distribution found in the 1935 Hensen samples is shown in Fig. 1. It is seen that the Channel, Southern Bight and the more northern part of the section have characteristic plankton populations. This distribution was repeated in 1936 and 1937 with the following modifications: in 1936, small copepods were found in the northern positions XI–XV as well as in the Channel positions II–VII. Small copepods were also found in all stations in 1937, but owing to pressure on the ship's time these stations did not extend farther north than position IX. *Phaeocystis* was found farther south in 1936 than in 1935 in positions V–XII, and in 1937 it was practically absent, traces only being found in position VIII. The area of large copepods was restricted to position XV in 1936, though it had extended as far south as position X in 1935.

SUMMARY

Phosphate, salinity and temperature records of waters of the North Sea and English Channel have been compared for April or May in the years 1935, 1936 and 1937, and the plankton distribution has been noted. Attention is called to the appearance of stability in certain features.

Thus, a high phosphate content was found to be associated with extremes of salinity and temperature, in similar areas in each year. The phosphate appears to be brought into the North Sea and Channel by oceanic water and by drainage from the land.

The plankton organisms were also similarly distributed in each year.

REFERENCES

ATKINS, W. R. G., 1930. Seasonal variations in the phosphate and silicate content of sea water in relation to the phytoplankton crop. Part V. November 1927 to April 1929, compared with earlier years from 1923. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 821–52.

COOPER, L. H. N., 1933. Chemical constituents of biological importance in the English Channel, November 1930 to January 1932. Part I. Phosphate, silicate, nitrate, nitrite, ammonia. *Journ. Mar. Biol. Assoc.* Vol. XVIII, pp. 677–728.

GRAHAM, M., 1936. The Lowestoft Photometer. *Journ. Cons. Int. Expl. Mer*, Vol. XI, pp. 205–10.

—— 1938. Phytoplankton and the herring. Part III. Distribution of phosphate in 1934–6. *Min. Agric. Fish., Fish. Invest.*, Ser. II, Vol. XVI; No. 3, pp. 1–26.

HARVEY, H. W., COOPER, L. H. N., LEBOUR, M. V. & RUSSELL, F. S., 1935. Plankton production and its control. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 407–41.

THE DISAPPEARANCE OF *ZOSTERA MARINA*

By W. R. G. Atkins, Sc.D., F.R.S.

Head of the Department of General Physiology at the Plymouth Laboratory

In his paper on "The autecology of *Zostera marina* in relation to its wasting disease", Tutin (1938) states that "In the British Isles the year 1931–2 showed a sunshine deficiency of about 20 % below normal, and no other year in the past ten showed a deficiency approaching this. The scanty figures available for other countries suggest that this unusual lack of sunshine was a general phenomenon, though in some countries it was less pronounced but of longer duration." His enquiries showed that about 1931 there was extensive mortality on the Atlantic coast of the U.S.A., though there was some evidence of a local decline in 1930. A year later, in 1932, *Zostera* had practically disappeared at Beaufort, North Carolina and as far north as Nova Scotia. In 1933 scarcity spread still farther northward to all localities in Canada. At Plymouth, England, the plant is believed to have begun to decrease towards the end of 1931. In § 6 of his summary Tutin writes: "It is suggested that the enfeeblement of the plant due to lack of sunshine in 1931–2 is the fundamental cause of the epidemic, and that recovery depends on the regeneration of the plant from seed and is therefore likely to proceed slowly."

It appeared desirable that this interesting suggestion should be tested by an extension of the examination of the meteorological records beyond ten years, as far as they go, namely back to 1897, and that the alleged 20 % deficiency should be checked. Accordingly, taking the sunshine normals as revised up to 1928, the amounts of sunshine received each year in each of the twelve districts of the British Isles were tabulated as percentages of the normal. As is customary mean values were obtained for the districts 1–10, namely excluding the north of Scotland (0) with adjacent islands, and the English Channel Islands (11). It appears unnecessary to give all the figures, especially as since 1928 such percentages have been published by the Meteorological Office on the 1928 basis, but the following comments may be made upon the records from 1897–1937 inclusive. The most striking thing in the series is the uniformity of the results. As regards low values, in 1898 Ireland S. had 81 % of its normal sunshine. In 1900 and 1902 England N.E. had 84 %, as had also Scotland E. in 1902. The year 1912 gave conspicuously low values, and averaged 83 % for the ten districts, Scotland E. and England N.E. showing 76 and 78 % respectively. In 1916 districts 0–4 inclusive showed 83–86 %. In 1920 England Midland, Scotland W. and Ireland S. had 84–86 %, and in 1924 Ireland S. had 84 %. In 1927 England M. had 82 %. In 1931, the year supposed to have been destructive for *Zostera*, England S.W. had 83 and England M. 85 %, both districts had 85 % in 1932 and England E.

had 85 %. In 1936 England S.W. had 85 % and in 1937 England E. had 84 %. There is obviously nothing very unusual in the low values which occurred in some districts in 1931 and 1932.

Turning to the high values, in 1899 England S.W. had 122 % of the normal sunshine with an average of 114, and in 1901 England N.W. had 119. England E. had 115 % in 1906 and England N.W. had 120 % in 1911, which averaged 115 %, the maximum average, followed by the minimum in 1912. England M. had 115 % in 1921 and England S.E. had 116 % in 1929 and 115 % in 1933.

Table I puts on record the values for the district including Plymouth, namely England S.W. and S. Wales, and the mean values for the ten British Isles districts as usually taken by the Meteorological Office. For neither are the low values of 1931–2 outstandingly low. They have been equalled or surpassed in earlier years.

TABLE I. PERCENTAGE OF NORMAL SUNSHINE

a, England S.W. and S. Wales (district No. 8) calculated on the normal value to 1928, namely 4·28 hr. a day.

b, The ten districts of the British Isles, calculated on the normal, 3·95 hr. a day.

	1897	1898	1899	1900	1901	1902	1903
a	106	109	122	111	111	97	98
b	104	97	114	100	111	93	94
	1904	1905	1906	1907	1908	1909	1910
a	99	101	110	98	102	109	98
b	99	104	111	98	99	104	97
	1911	1912	1913	1914	1915	1916	1917
a	118	81	91	104	101	96	99
b	115	83	91	104	102	89	98
	1918	1919	1920	1921	1922	1923	1924
a	104	105	85	111	97	95	89
b	100	103	90	111	98	96	91
	1925	1926	1927	1928	1929	1930	1931
a	105	93	91	99	113	90	83
b	101	94	93	101	109	95	89
	1932	1933	1934	1935	1936	1937	
a	85	107	100	97	85	88	
b	89	106	102	104	93	90	

Table II shows the normal values for the hours of sunshine for the ten districts and the corresponding percentages calculated with respect to the maximum, England S.E., and to the mean. The value for the north of Ireland 3·51 hr. is only 78 % of the maximum, and only 89 % of the mean. In spite of this *Zostera* formerly grew well in the north of Ireland, though a reduction of sunshine to 89 % of the mean is suggested as having been the cause of the fatal nature of the *Zostera* disease.

Furthermore, the illumination due to sunshine in the north of Ireland or of Scotland is on the average less than that in the south of England in which with a midsummer maximum solar altitude of 63°, for latitude 50°, the vertical component of the light from sun and sky is about 122 kilolux (Atkins, Ball & Poole, 1937); for the north of Ireland, around latitude 55°, the maximum altitude is 58°, so the illumination is about 117 kl., similarly with altitude 55° in the north of Scotland the maximum illumination is around 110 kl. This is to some extent offset by the longer duration of daylight during the summer, though the vertical illumination from a low angle sun is small. *Zostera* has been reported as growing (Börgesen, 1903) as far north as 61° 28′ N. in 2–4 m. of water in Vaagfjord in Syderö, the most southerly of the Faeröes. The mean sea temperature at the adjacent Thorshaven is 7·8° C. with minimum 5·4° and maximum 10·6°. No sunshine records are available for the Faeröes.

Table II. Normal sunshine (1928) and percentages calculated on the maximum and mean values

District	Hours	%	%
Scotland E.	3·63	81	92
England N.E.	3·93	87	100
England E.	4·32	96	109
England M.	3·82	85	97
England S.E.	**4·49**	100	114
Scotland W.	3·70	82	94
England N.W. and N. Wales	3·89	87	99
England S.W. and S. Wales	4·28	95	108
Ireland N.	3·51	78	89
Ireland S.	3·96	88	100
Mean	3·95	88	100

But the assumption that a greater duration of sunlight necessarily means a greater amount of light is not correct. It has been shown (Atkins, 1938) that though the relation usually holds over a year, it does not always do so, for the altitude of the sun when clear is of great importance. According to photo-electric measurements made at Plymouth the year 1931 stood third on the list of eight years 1930–7, as regards the amount of light received, and 1932 was almost identical with four of the other years. Furthermore, the radiation records at London show that in 1931 the amount received was not unusually low but rather above normal.

Finally, with a water plant, one has to consider the extinction coefficient of the water. In estuarine and coastal waters this is subject to large variations, from about 0·2 to 2·5 even in June, thus introducing more than a tenfold variation in the amount of light reaching the plants (Poole & Atkins, 1937; Cooper & Milne, 1938).

At Plymouth *Zostera* has been under observation since the opening of the laboratory, as it was always exhibited in one of the aquarium tanks. I am indebted to Dr E. J. Allen for the information that never within his 42 years' experience was there a scarcity of *Zostera* in any way comparable to the shortage of the last few years. There is certainly no ground for attributing its disappearance to any decrease in illumination leaving the plant, thus weakened, an easier prey to disease.

SUMMARY

The suggestion that the enfeeblement of *Zostera marina* due to lack of sunshine in 1931–2 is the fundamental cause of the epidemic is not supported by the meteorological data available from 1897 onwards, or by the known extinction coefficients of the water.

REFERENCES

ATKINS, W. R. G., 1938. Photo-electric measurements of the seasonal variations in daylight around 0·41 mμ. from 1930 to 1937. *Proc. Roy. Soc.* A, Vol. 165, pp. 453–65.

ATKINS, W. R. G., BALL, N. G. & POOLE, H. H., 1937. The photo-electric measurement of the diurnal variations in daylight in temperate and tropical regions. *Proc. Roy. Soc.* A, Vol. 160, pp. 526–39.

BÖRGESEN, F., 1903. *Botany of the Faeröes*, Vol. 2, p. 706.

COOPER, L. H. N. & MILNE, A., 1938. The ecology of the Tamar estuary. II. Underwater illumination. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 509–28.

POOLE, H. H. & ATKINS, W. R. G., 1937. The penetration into the sea of light of various wave-lengths as measured by emission or rectifier photo-electric cells. *Proc. Roy. Soc.* B, Vol. 123, pp. 151–65.

TUTIN, T. G., 1938. The autecology of *Zostera marina* in relation to its wasting disease. *New Phytologist*, Vol. XXXVII, pp. 50–71.

A REVISION OF THE AMPHIPOD GENUS *BATHYPOREIA* LINDSTRÖM

By E. Emrys Watkin, B.Sc., Ph.D.

Lecturer in Zoology, University College of Wales, Aberystwyth

(Text-figs. 1–6)

CONTENTS

	PAGE
History of the Genus	211
Notes on the Structural Characters of the Genus	214
Description of the Species	216
B. guilliamsoniana (Bate)	216
B. pelagica (Bate)	219
B. elegans, nom.nov.	222
B. tenuipes Meinert	225
B. gracilis Sars	227
B. pilosa Lindström	228
B. sarsi, nom.nov.	231
B. lindströmi Stebbing	234
Key to the Identification of the Species	234
Acknowledgements	235
References	235

History of the Genus

The genus *Bathyporeia* was established by Lindström (1855, p. 59) on specimens collected in the Baltic at Wisby and Landskrona. His description is based, apart from a reference to the epimera as small and beset with hairs, on the form of the appendages. He assigned to the genus one species, *pilosa*, in which the segments of the body are described as smooth, the form generally rounded, the eyes black, small and somewhat reniform, and the length under three lines. He gives a detailed description and drawing of the appendages. From the description of the antennae and of the eyes it may be assumed that the specimens were females.

Spence Bate in 1856 (p. 59), and again in 1857*a* (p. 146), unaware of Lindström's paper, described a new genus, *Thersites*, as follows: "The upper antennae with the second joint of the peduncle produced from the inferior side of the first. Second gnathopod terminating in a bush. Telson double." He assigned to the genus two species, namely, *guilliamsoniana* with "the inferior antenna as long again as the superior" and *pelagica* with "the inferior antenna six times as long as the superior". Thus Bate was describing a female specimen in *guilliamsoniana* and a male in *pelagica*. Later (1857*b*, p. 271) he pointed out that his genus *Thersites* lapsed in favour of *Bathy-*

poreia, and that his species *guilliamsoniana* was probably the same as the *pilosa* of Lindström.

In 1862 (p. 174) Bate gave more extensive descriptions of the two species *pilosa* and *pelagica*, based on imperfect specimens, and added a third species, *robertsoni*, based on imperfect male specimens obtained in February at Cumbrae from low-water pools. The distinction between *pelagica* and *robertsoni* is based mainly on the length of the flagellum of the antenna which in the former is "longer than the animal", and in the latter about "half as long as the animal", and in the diagram shown as having twenty-four articulations bearing calceoli. Bate and Westwood in 1863 (pp. 304–10) gave further descriptions of these three forms.

Stebbing (1875, p. 74), on an examination of living specimens from the north Wales coast and from the English Channel coast, came to the conclusion that all three of Bate's species were referable to one species, the *pilosa* of Lindström, with *pilosa* as the adult female, *pelagica* as the adult male and *robertsoni* as the young male. He collected specimens indiscriminately over the whole intertidal area; evidence is now available to show that the various species are definitely zoned in relation to tide levels. Stebbing further commented on the scarcity of forms with long antennae, i.e. the adult males; this is a feature common to all the species in the genus.

Meinert (1877, p. 201) also expressed the opinion that the *pelagica* and *robertsoni* of Bate should be referred to the *pilosa* of Lindström. However, he described a new species, *tenuipes*, which Sars later (1891, p. 129) regarded as a synonym of *pelagica*.

Blanc (1884) agreed with Stebbing and Meinert, but Chevreux (1887) upheld *robertsoni* as a distinct species.

Sars (1891, pp. 127–34) gave detailed descriptions of five species of this genus, four of which occur in the fauna of Norway, namely *norvegica*, *pelagica*, *gracilis* and *robertsoni*. *B. norvegica* is described as a new species occurring in fine sand at a depth of 2–6 m. in south Norway, *pelagica* as occurring along the whole of the Norwegian coast within the littoral zone and associated with *norvegica*; *gracilis* as a new species of which he had one male and one female specimen occurring in deep water off the west coast; *robertsoni* from three male specimens obtained on the west coast of Finmark. He further described *pilosa* from specimens in the Stockholm museum, and this is referred to as a Baltic species with no known ex-Scandinavian distribution. Sars pointed out the taxonomic value of the coxal plates, of the third epimeral plate and of the armature of the fourth pleon segment on which later Stebbing established a key for the separation of the species.

Della Valle (1893, pp. 751–54) accepted *norvegica* as a distinct species but referred *pelagica*, *robertsoni* and *gracilis* to the *pilosa* of Lindström.

Scott (1893, p. 213) referred to *norvegica*, *pelagica* and *robertsoni* as occurring in the fauna of the Firth of Forth, thus accepting the species as described by Sars.

Walker (1895*a*) examined the specimens of this genus in the British

Museum collections which were presumably determined by Spence Bate. His remarks are as follows:

> "*Bathyporeia pilosa* (Lindström).
>
> "Two tubes so labelled, of these No. 50 contains two females of *B. norvegica* (Sars); the other No. 85 contains eleven specimens, all of which have dark eyes; some have dorsal spinules on the fourth pleon segment, others have not; one (a large female) has a rudimentary tooth slightly in front of the rounded hind margin of the third pleon segment.
>
> "*Bathyporeia pelagica* (Bate). One adult male 5 millim. long.
>
> "This agrees with the form described by Sars under the above name. It must be confessed that, of the five species of *Bathyporeia* given by Sars, only *B. norvegica* (Sars) seems to be distinct, owing to its having the hinder angle of the third pleon segment produced to a point, instead of being rounded, as in the other species."

Walker later (1895*b*, p. 295) expressed the opinion that the species *pelagica*, *robertsoni* and *gracilis* should be referred to the *pilosa* of Lindström.

Norman (1900, p. 326) stated that he could not "regard some of the forms as entitled to specific, indeed they seem hardly worthy of varietal, separation". He refers to the species *norvegica*, *pelagica*, *robertsoni* and *gracilis* but does not state which he regards as specific. In a later paper (1905, p. 82) he assigns *norvegica* as a synonym of *guilliamsoniana.*

Stebbing (1906, pp. 119–22) accepted the five species as described by Sars and added a sixth doubtful species, *lindströmi*, based on Della Valle's description of the Mediterranean forms. He accepts *norvegica* as a synonym of *guilliamsoniana*, based on Walker's statement that the finest specimens in the Spence Bate collection are similar to the *norvegica* of Sars.

Chevreux & Fage (1925, pp. 91–5) described and referred to *guilliamsoniana*, *pelagica* and *robertsoni* as occurring on the coast of France.

Stephensen (1928, p. 130–32) described and referred to *guilliamsoniana*, *pelagica* and *robertsoni* as occurring in the fauna of Denmark, with *pilosa* as a Baltic species.

In the above survey of the history of the genus, reference is made only to those papers which have contributed to the morphology and nomenclature of the species. In the survey of the species which follows reference is also restricted to those papers which describe or figure specimens I have had the opportunity of examining. A reference is omitted if I have not examined the specimens or cannot satisfy myself as to the identity of the species referred to. The survey of the geographical distribution of the species is based almost entirely on the examination of specimens in various collections and on personal collection; it is not based on reference to the species in the literature.

This genus is abundant in the intertidal sands around all the shores of Britain and occurs generally distributed around the coasts of Europe extending into comparatively deep water. Raitt (1937, p. 249) has shown that it is abundant in the Petersen grab hauls taken in the north-western North Sea and adjacent waters and in the stomachs of haddock, forming a considerable item in their diet.

The genus is easily identified by the geniculate character of the first antenna and the spatulate nature of the second gnathopod. Sars (1891, p. 127), Stebbing (1906, p. 119), Chevreux & Fage (1925, p. 91) give adequate descriptions of the genus. I hope to publish shortly a description of the feeding mechanism and burrowing habits of some of the species.

Notes on the Structural Characters of the Genus

The species in the genus are remarkably similar in their structural characters, a fact which has led to their confusion one with another. The chief distinguishing characters are relatively minor ones, the form of the coxal and epimeral plates, the presence or absence of spines on the fourth pleon segment, the shape of certain joints of the appendages and their relative size in relation to succeeding joints, the form of the body, the colour of the eyes and of the eggs, and the extent of the body pigmentation. The sensory armature of the species follows very closely that described by Sexton (1925, pp. 358–60) for *Gammarus chevreuxi* and is remarkably constant in the various species. It affords little of specific value so that a generalized description will serve for all the species. Only the armatures of those parts of the body used in the identification of the species is given. The differences between the sexes, apart from the brood plates, are well marked in the adult stages, particularly in the characters of the antennules and antennae.

Antennule. The large truncated basal joint shows a considerable degree of variation in the shape of its apex, which character may be used as specific. The dorsal surface of this joint carries a sensory groove in which lies a group of plumose hairs which Sexton (1925) regards as probably analogous to the auditory sac of *Anaspides* and many Decapoda. On the ventral surface is a group of feathered hairs varying in number from two to five in the various species, and two plumose hairs set at an angle of 90° to each other with a series of bristles immediately dorsal to them. On the ventral surface at the apex is a group of spines, each with a bifid tip and a small flagellum near the apex. No attempt is here made to distinguish between pointed spines, slender spines and spines. The second joint is characteristically elbowed in relation to the first joint and bears distally a group of spines dorsally and a group of spines or of bristles ventrally. The third joint is like the second. The number of joints in the flagellum is of some specific value and it shows distinct "secondary sexual characteristics".

In the male each joint carries distally a calceolus with an associated group of setae dorsally and a group of aesthetascs ventrally, however, the last one or two joints do not bear calceoli. In the female the number of joints is less, and the number of aesthetascs per joint is less. The accessory flagellum has two joints, the basal of which bears up to four groups of two spines each on the inner margin, with a single spine at the distal dorsal apex in both male and female; the male in addition has a tuft of setae on the middle of the outer margin. The size relation of the basal joint to the second joint is of specific value; the second joint is unarmed apart from a tuft of setae at the apex.

ANTENNA. The third joint is short and broad and carries two groups of bristles on its anterior margin. The fourth joint is twice as long as the third and bears groups of bristles on both anterior and posterior margins; the third and fourth joints may bear an occasional plumose hair. The fifth joint is less than the fourth and with bristles on the anterior and posterior margins. The flagellum shows secondary sexual characteristics in the male. The flagellum of the adult male is considerably elongated, its length in relation to the size of the body is of specific value. Each joint apart from the last one or two carries at the apex a calceolus and a tuft of setae. In the female the number of joints is few, and they are not modified in any way; the length of the flagellum in relation to the last two joints of the peduncle is of some specific value.

GNATHOPOD I. The shape of the propodus is of some specific value. Generally it is oval in outline with the posterior border carrying a long series of hairs and the anterior border some groups of bristles. The inner surface bears a row of spines diagonally placed, and the outer surface a few scattered bristles. The shape, size and armature of the propodus in male and female are alike. The dactylus is claw-like and larger in the male than the female; its anterior border carries a bristle which is modified in the fully adult form to a serrated bristle; the posterior border has an unmodified bristle.

PERAEOPOD III. The basis is much expanded with a row of bristles along the anterior and posterior margins and with five groups of spines on the outer surface near the anterior margin. The bristles of the anterior margin gradually change to feathered bristles near the ischium. The ischium is small and bears a group of bristles distally and feathered bristles on its anterior margin. The merus is characteristically expanded and its shape is of specific value. Its anterior margin is heavily clothed with a row of feathered bristles which become modified to serrated feathered bristles near the carpus. The number of feathered bristles is usually greater in the female than in the male. The outer surface near the anterior edge carries a row of spines. The carpus and propodus are reduced and the dactylus is absent. The carpus bears a number of spines along the anterior edge, the propodus a number of bristles along its anterior edge and one spine on the outer surface apically.

PERAEOPOD V. The size relation of the carpus and propodus is of some specific value. The dactylus is much reduced and is surrounded by a group of spines from the apex of the propodus. The carpus carries groups of bristles and spines on its anterior and posterior margins. The propodus carries groups of spines on the anterior margin and on the outer face.

UROPOD III. The basal joint carries groups of bristles along its outer margin and a row of spines at the apex. The inner ramus is much reduced, with a few serrated spines at its apex. The outer ramus carries numerous feathered bristles along the inner margin and in some species an ordinary bristle associated with some of the groups of feathered bristles; the outer margin carries groups of spines. The terminal joint has the same armature as the basal joint. The shape of the first joint of the outer ramus and its size in relation to the second is of specific value.

Telson. In all species the telson is cleft almost to the base. The armature is remarkably constant and gives little of specific value. Each half carries at the apex, from within outwards, a group of bristles which vary in number from two to six according to age and species, a group of usually two spines, a group of one or two serrated spines, and finally a group of one to three bristles. The dorsal surface carries one plumose hair apically, one a third of the distance from the apex and one nearer the base. The outer margin carries a further group of serrated spines and bristles, which increase in number with age. The variation in the number of bristles and spines with age in each species is such that this character, which has previously been given specific value, cannot be a determining one.

Pleon segment IV. This segment is grooved dorsally, the groove in the adult male is considerably deeper than in the adult female. The posterior edge of the groove carries a pair of forwardly directed bristles which are better developed in the male than in the female. In some species this segment also carries a pair of backwardly directed spines.

Description of the Species

B. guilliamsoniana (Bate) (Fig. 1 *a–g*)

Thersites guilliamsonia Bate, 1856, p. 59.
T. guilliamsoniana Bate, 1857*a*, p. 146.
Bathyporeia guilliamsonia Bate, 1857*b*, p. 271.
B. pilosa Bate, 1862, p. 172, pl. 31, f. 4; Bate & Westwood, 1863, p. 304.
B. norvegica Sars, 1891, p. 128, pl. 43; Della Valle, 1893, p. 754; Scott, 1893, p. 213, pl. 5, f. 22; Walker, 1895*a*, p. 470; Walker, 1895*b*, p. 295.
B. guilliamsoniana Norman, 1905, p. 82; Stebbing, 1906, p. 120; Chevreux & Fage, 1925, p. 92, f. 84, 85; Stephensen, 1928, p. 130, f. 25.

It is now impossible to be certain if the two female specimens in tube no. 50 of the Spence Bate collection are the type specimens (see p. 213). Bate refers to the type specimens as having a length of $\frac{2}{20}$ inch, this is either an error or the above two female specimens are not the type specimens.

The description and drawings of this form as given by Sars are reasonably adequate, so that a brief description of certain appendages only is required.

Male. First pair of coxal plates with a pointed tip and carrying a group of up to six bristles on the posterior margin; the origin of a smaller bristle is marked by a well-defined tooth. Second and third pair of coxal plates with a well-defined tooth at the posterior corners, marked by a distinct sulcus; the ventral margin bears a row of about fifteen to twenty bristles. Fourth pair of coxal plates rounded as in the other species but carrying up to forty-eight bristles on the ventral margin. Last pair of epimeral plates (pleon segment III) with a distinct tooth at the posterior corner which projects beyond the posterior vertical margin of the plate; in fully adult males this tooth is considerably reduced and traces of it only remain; the outer margin bears four or five groups of spines which may be serrated in fully adult forms. Pleon segment IV deeply depressed with a pair of forwardly curving bristles and a pair of backwardly directed spines. The basal joint of the antennule is evenly rounded at the tip, its lower border with four or five feathered hairs; the flagellum is of ten to twelve joints of which the first eight to ten carry a calceolus and a dense tuft of aesthetascs; the basal joint of the accessory flagellum is long and narrow, as 100 : 14, with the second joint about a third the length of the first, with five groups of spines on the inner margin and a tuft of bristles on the outer margin. The antenna and first gnathopod are as described by Sars. Peraeopod III with the merus twice as long as broad, as 100 : 50, with the relation of the length of the merus to carpus plus propodus combined as 100 : 75. The propodus and carpus of peraeopod V are of equal length, robust and very spiny, dactylus short. Uropod III with the second joint of the outer ramus less than a third the length of the basal, as 30 : 100, with fifteen to seventeen feathered bristles on the inner margin of the basal joint and three to four on the second joint, with nine groups of spines on the outer margin. Telson with the typical arrangement of apical armature of which an average condition is, reading from within outwards, five or six bristles, two spines, one plumose hair (inset on dorsal surface), one or two serrated bristles, one to three bristles; laterally four serrated bristles and two bristles.

Female. The female differs from the male in the following points: flagellum of antennule with seven or eight joints, the accessory flagellum without a tuft of setae on outer margin; flagellum of the antenna with eight or nine joints, considerably shorter than the fourth and fifth joints of the peduncle combined, as 71 : 100. The merus of peraeopod III may carry up to forty feathered bristles on its anterior border. Uropod III with a less number of feathered bristles, usually ten to twelve. Pleon segment IV less deeply depressed.

This species attains a length of 8 mm., and is the largest and most robust in the genus. It is translucent without any trace of pigment apart from the eyes which are a bright red. Eggs with a yellowish tinge.

Geographically this species is probably distributed around all the shores of Europe apart from the Baltic. Chevreux & Fage (1925, p. 92) have recorded it from numerous localities in the English Channel and Mediterranean waters; Stephensen (1926, p. 53 and 1928, p. 130) from numerous localities around the Danish coasts; Elmhirst (1931, p. 170) from numerous localities around the Scottish coasts; Raitt (1937, p. 249) as present in many of the Petersen grab hauls from the north-western North Sea to a depth of 75 m. and in the stomachs of haddock to a depth of 35 m.; Crawford (1937*a*,

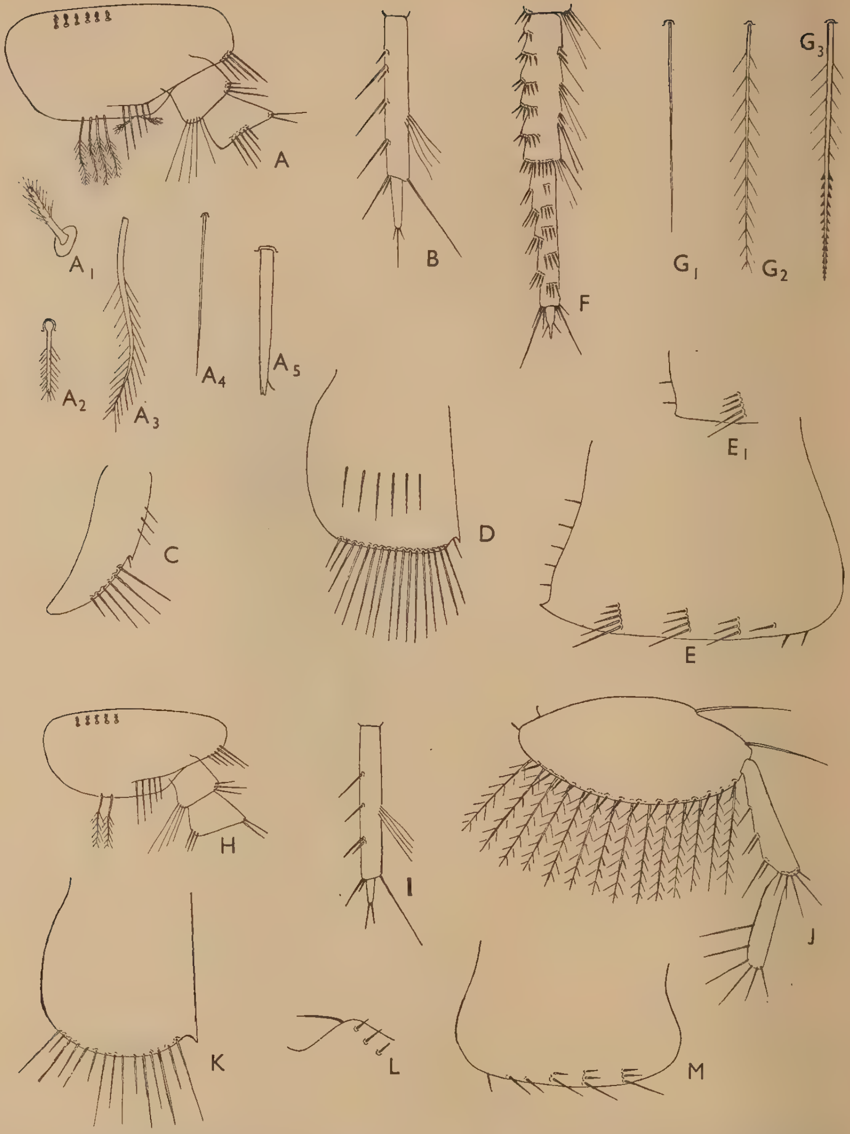


Fig. 1. *a–g*, *B. guilliamsoniana* ♂. *h–m*, *B. gracilis* ♂ type specimen. *a*, Basal joint of antennule; a_1, Plumose hair from dorsal groove; a_2, a_3 and a_4, Plumose hair, feathered hair and bristle from ventral margin; a_5, Spine from apex of joint. *b*, Accessory flagellum of antennule. *c*, First coxal plate. *d*, Second coxal plate. *e*, Third epimeral plate in adult ♀ and young ♂. e_1, Third epimeral plate in adult ♂. *f*, Carpus, propodus and dactylus of peraeopod V. g_1, g_2, g_3, To show change from bristle to feathered bristle to feathered serrated bristle along anterior margin of basis, ischus and merus of peraeopod III. *h*, basal joint of antennule. *i*, Accessory flagellum of antennule. *j*, Merus, carpus and propodus of paraeopod III. *k*, Second coxal plate. *l*, Fourth pleon segment. *m*, third epimeral plate.

p. 637) from Plymouth waters; Moore (1937, p. 118) from Isle of Man waters. In the Norman collection in the British Museum there are specimens from the Moray Firth (register numbers 13762–781 and 13803), from Ilfracombe (13792) and from Guernsey (13782–791). As *B. norvegica* Sars (1891, p. 128) has recorded it from a single locality in the south of Norway; Della Valle (1893, p. 754) from the Bay of Naples; Scott (1893, p. 213) from the Firth of Forth; Walker (1895*b*, p. 295) from the north Wales and Isle of Man coasts. Spence Bate (1863, p. 306) gives the type locality as Weymouth "on a fine sandy bottom", and Tenby. This species may be collected at the low-water mark of spring tides and in shallow water at many localities around the British coasts.

B. pelagica (Bate) (Fig. 2)

Thersites pelagica Bate, 1856, p. 59; 1857*a*, p. 146.
Bathyporeia pelagica Bate, 1862, p. 174, pl. 31, f. 6; Bate & Westwood, 1863, p. 309.

Type specimen, a male, 5 mm. long, in the Spence Bate collection, British Museum, tube no. 86. Locality, Bate (1863, p. 309), Moray Firth.

MALE. This description is based partly on the type specimen (as far as possible without dissection) and partly on specimens collected at Aberystwyth and Kames Bay, Millport, and compared with specimens from other localities.

Body robust. First pair of coxal plates with a rounded tip and carrying a row of three to four bristles on the posterior margin; the origin of a more dorsally situated bristle is not marked by a tooth. Coxal plates II, III and IV as deep as the corresponding segments. Second pair of coxal plates rounded anteriorly without a tooth at the posterior corner; this corner is marked by a rounded projection not defined by a sulcus; the ventral margin carries a row of six to nine bristles. Third pair of coxal plates rectangular in outline, otherwise much as the second pair. Fourth pair of coxal plates rounded as in the other species with about 24 bristles on ventral margin. Last pair of epimeral plates (pleon segment III) unevenly rounded at the posterior corner in the adult male but with a small tooth marked by a well-defined sulcus some little distance from the apex in the young male; the ventral border carries about four groups of spines, the number of spines per row decreasing anteriorly. Pleon segment IV deeply depressed dorsally and carrying a pair of stout spines directed posteriorly and a pair of bristles directed anteriorly. Antennules with the basal joint produced to a point dorsally—the somewhat triangular apex is characteristic of this species and of *tenuipes*—lower border with three feathered hairs. The flagellum is of nine to eleven joints of which the first eight to ten carry calceoli and each a dense tuft of aesthetascs; accessory flagellum with the second joint about a quarter the length of the basal, as 27 : 100; the basal carries three or four groups of two spines each on the inner margin and a tuft of setae on the outer margin. The flagellum of the antenna is longer than the body; all the joints except the last one or two carry calceoli. The propodus of the first gnathopod is an oblong oval as in the other species,

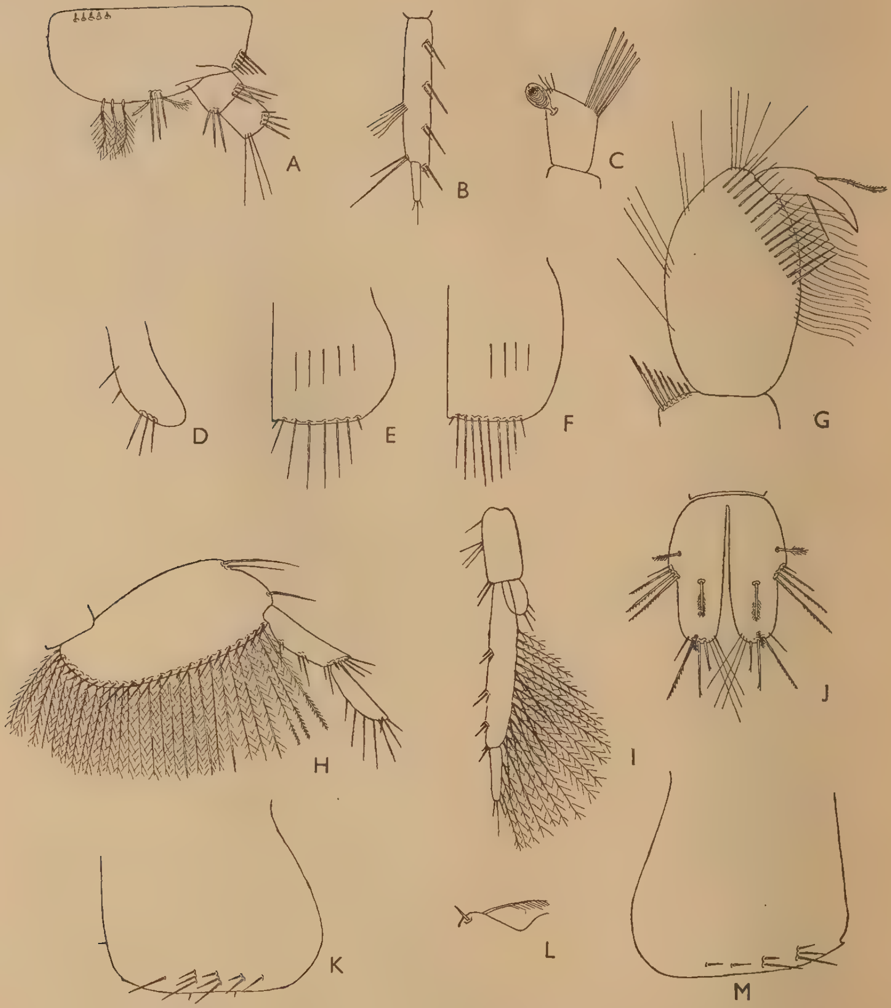


Fig. 2. *B. pelagica* ♂. *a*, Basal joint of antennule. *b*, Accessory flagellum of antennule. *c*, Typical joint from middle of flagellum of antennule. *d*, First coxal plate. *e*, Second coxal plate. *f*, Third coxal plate. *g*, Propodus and dactylus of first gnathopod. *h*, Merus, ischus and propodus of peraeopod III. *i*, Third uropod. *j*, Telson. *k*, Third epimeral plate in adult ♂. *l*, Fourth pleon segment in adult ♂. *m*, Third epimeral plate in adult ♀ and young ♂.

except *elegans*; the dactylus is sharply pointed and carries a feathered bristle on its anterior margin in fully developed males but a simple seta in mature but not fully developed males. Peraeopod III with the merus more than twice as long as broad, as 100 : 44, the relation of the length of the merus to carpus and propodus combined being as 100 : 74; the anterior border of the merus carries up to thirty feathered bristles on its edge with up to twenty-four spines on the outer face. Peraeopods IV and V elongate, the relation of the length of the carpus to propodus in peraeopod V as 81 : 100. The outer ramus of uropod III with the second joint about a third the length of the basal, as 37 : 100, with fourteen to sixteen feathered bristles on inner margin of basal joint and two to four on the second joint; an ordinary bristle is associated with several of the feathered bristles, outer margin with four or five groups of spines. Telson with the typical arrangement of apical armature of which the usual condition is, reading from within outwards, three to five bristles, two spines, one plumose hair, one serrated bristle, one bristle; laterally with two or three serrated bristles and one or two bristles. Eyes reniform with dark red pigment.

FEMALE. The female differs from the male in the following points: the flagellum of the antennule with six or seven joints, the accessory flagellum without a tuft of setae on its outer margin. The flagellum of the antenna with eight to eleven joints and a little less in length than the fourth and fifth joints of the peduncle combines, as 92 : 100. The merus of peraeopod III may carry up to thirty-four feathered bristles on its anterior margin, although this number is exceedingly variable in egg-bearing females, the minimum count was twenty-one. The outer ramus of uropod III carries a less number of feathered bristles, usually seven to ten. Last pair of epimeral plates as in the young male and with a variable number of groups of spines and spines per group, an examination of ten individuals gave the following readings: 2.2.1, 2.2.2, 3.2, 3.2.1 (twice), 3.3.2, 3.2.2.1, 3.3.1.1, 3.3.2.1, 3.3.1. The number of bristles on the ventral margin of the coxal plates is greater than in the male. The fourth pleon segment is less deeply depressed. Eyes rounded with dark red pigment.

The body pigment is abundant, particularly in the pleon and its appendages, but this is variable in specimens from various localities. Eggs deep blue in colour.

The distribution of this species is, as far as my present records are concerned, restricted to the intertidal sandy shores of the coasts of Britain. It is found to occupy a definite tidal level below the high-water mark of neap tides. It has been found at numerous points on the west coast of Wales, at Redcar (Yorkshire) and the extensive collections of the Scottish Marine Biological Station show it to be common in many localities around the Scottish coast. It has not appeared in the collections of the Copenhagen, Stockholm and Oslo Museums.

B. elegans*, nom.nov. (Fig. 3)

B. pelagica Sars, 1891, p. 129, pl. 44, f. 1.

Type specimens, numerous adult males and females, and young forms in the Zoological Museum, Oslo. Locality "in the Ognebugt off Jaederen", South Norway (Sars, 1891, p. 45).

The description given by Sars may be modified and amplified in the following particulars. Of the species in this genus this is the smallest and finest. The body is narrow and elongate; occasional specimens may reach a length of 6 mm., although 4–5 mm. is much more usual.

MALE. First pair of coxal plates with an obtusely pointed tip; the posterior margin carries a row of four to five bristles with a single bristle dorsal to the row, the origin of which is marked by a distinct but small tooth. The second, third and fourth pairs of coxal plates as deep as the corresponding segments. Second pair of coxal plates with a tooth on the posterior corner which is not as well developed as in *guilliamsoniana* and *tenuipes*; the tooth does not reach to the level of the base of the plate, but is variable in the degree of its development; the ventral margin carries a row of about twelve bristles. Third pair of coxal plates rectangular in outline, otherwise as the second pair. Fourth pair of coxal plates rounded as in the other species with about twenty-four bristles on the ventral margin. Last pair of epimeral plates (pleon segment III) rounded, without a tooth at the posterior corner; the outer edge carries about four groups of setae decreasing in number anteriorly. Pleon segment IV deeply depressed dorsally with one pair of bristles directed anteriorly and one pair of spines posteriorly. The basal joint of the antennule is evenly rounded at the tip, the lower border with two or three feathered hairs. Flagellum of nine to eleven joints of which the first seven to nine carry calceoli and a dense tuft of aesthetascs. Accessory flagellum with the second joint about a third the length of the basal, as 33 : 100; the basal carries up to four groups of spines on the inner margin and a tuft of setae on the middle of the outer margin. The flagellum of the antenna is longer than the body. The propodus of the first gnathopod is an oblong oval about twice as long as broad, longer than in the other species. The merus of peraeopod III is more than twice as long as broad, as 100 : 46, the relation of the length of the merus to carpus and propodus combined being as 100 : 87; anterior border of the merus with about twenty-four feathered bristles and with about twenty-four spines on the outer face. Peraeopod V with the carpus not so long as the propodus, as 90 : 100, dactylus pointed as a spine. The second joint of the outer ramus of uropod III is a little more than a third the length of the basal, as 100 : 38; the basal carries nine to eleven feathered bristles on its inner margin with an accessory seta associated with some of the bristles, the second joint

---

* Mr G. I. Crawford desires me to state that his reference to *B. elegans*, this *Journal*, Vol. XXI, p. 639, line 4, is an error and should read *B. gracilis*.

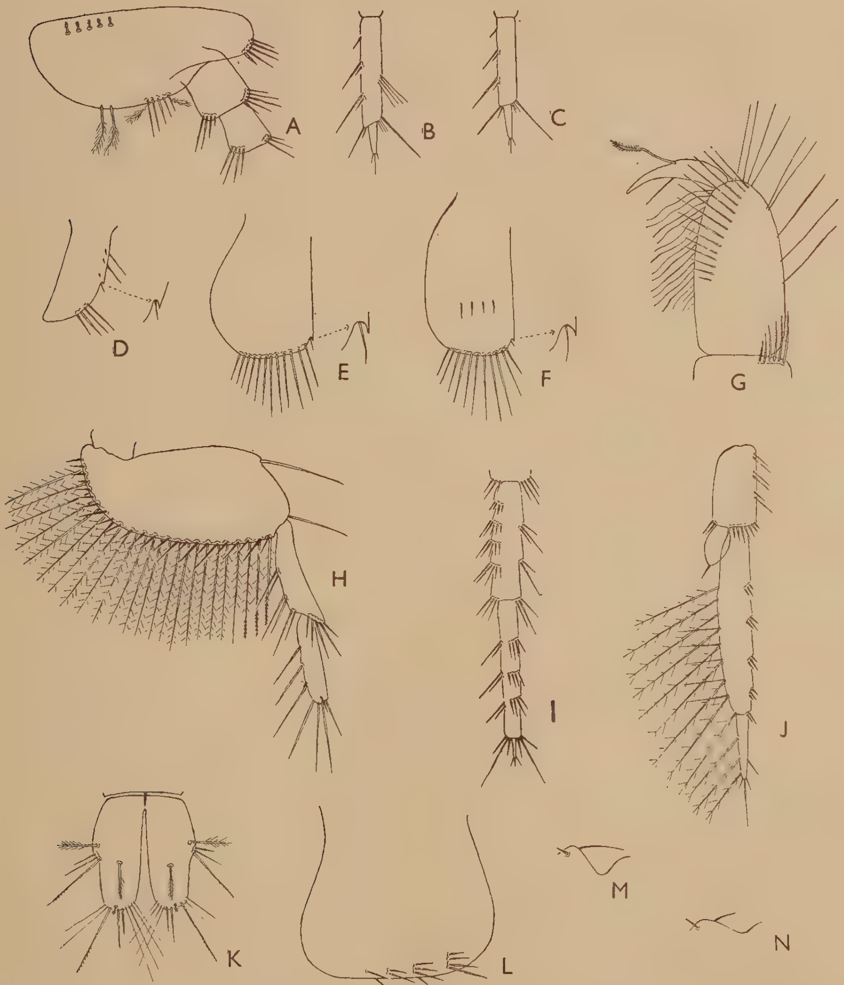


Fig. 3. *B. elegans* ♂. *a*, Basal joint of antennule. *b*, accessory flagellum of ♂. *c*, Accessory flagellum of ♀. *d*, First coxal plate. *e*, Second coxal plate. *f*, Third coxal plate. *g*, Propodus and dactylus of first gnathopod. *h*, Merus, carpus and propodus of peraeopod III. *i*, Carpus, propodus and dactylus of peraeopod V. *j*, Third uropod. *k*, Telson. *l*, Third epimeral plate. *m*, Fourth pleon segment in ♂. *n*, Fourth pleon segment in ♀.

with two or three feathered bristles; the outer margin bears four to six groups of spines. Telson with the typical arrangement of apical armature of which a usual condition is, reading from within outwards, two to four bristles, two spines, one plumose hair, one to three bristles, and laterally one or two serrated bristles and two or three bristles. Eyes large and reniform with bright red pigment.

FEMALE. The female differs from the male in the following points: the flagellum of the antennule with six joints, occasionally five, accessory flagellum with the basal joint shorter and broader, giving a relation with the second joint as 100 : 42 and without a tuft of setae on its outer margin. The flagellum of the antenna has eight or nine joints, occasionally ten, the relation of the length of the flagellum to the fourth and fifth joints of the peduncle being as 88 : 100.

The feathered bristles on the inner margin of uropod III are about equal in number to those in the male but are not so well developed. The merus of peraeopod III has up to thirty feathered bristles on the ventral margin. The third epimeral plate gave the following readings for spine groups: 4.2.1 (twice), 4.2.2, 4.3.1 (twice), 4.3.2, 4.1.1.1, 5.3.2 (twice). The fourth pleon segment is less deeply depressed. Eyes rounded with bright red pigment.

The body in both male and female is translucent with practically no pigment. The colour of the eggs is yellowish.

Thus the main points in which *elegans* differs from *pelagica* are (i) the shape of the basal joint of the antennule, (ii) the presence of a small tooth on the coxal plates, (iii) the rounded posterior border of epimeral plate III, (iv) the general lack of pigmentation, (v) the colour of the eggs and of the ovary in the female, and (vi) the distribution in relation to tide level.

This species may be collected at low-water mark of spring tides in several localities around the coasts of Britain. It is in general a shallow-water form. The collections of the Oslo Museum show it to be present in several localities along the whole Norwegian coast, the Copenhagen Museum collections contain specimens from the Kattegat and from the North Sea coast of Denmark. In the Norman collection in the British Museum there are specimens from the Moray Firth (register numbers 13762–781 and 13826–827), from "25 miles off the Isle of May" (13813–816), from Whitsand Bay (13828–842), from Shetland (13843–845), and from Cumbrae (13846–855). Crawford (1937*a*, p. 637) records it as *B. pelagica* from Plymouth waters. The extensive collections of the Scottish Marine Biological Station show it to occur in several localities on the east and west coasts of Scotland and I have found it in one locality on the west coast of Wales. Stephensen (1928, p. 131) records *B. pelagica* as far south as Madeira, but this record needs confirmation in view of its possible confusion with *tenuipes*. Thus it may be stated to have a general distribution around all the Atlantic coasts of Europe.

B. tenuipes Meinert (Fig. 4)

B. tenuipes Meinert, 1877, p. 201.
B. gracilis Norman, 1900, p. 326.
B. elegans Crawford, 1937 *a*, p. 639.

Type specimen, an adult male in the Zoological Museum, Copenhagen. Locality given on label in tube as Anholt, Kattegat. Meinert's description is as follows: "Antennae superiores subundae, flagello appendiculari biarticulato. Antennae inferiores articulo tertio et quarto longis atque tenuibus. Angulus capitis acutus productus. Pedes omnes tenues, modice hirsuti; pedes saltatorii ultimi paris setis simplicibus instructi."

Through the kindness of Dr K. Stephensen of Copenhagen I have been able to examine the type specimen of *tenuipes* and find it sufficiently different from *B. pelagica* (Bate) and *B. elegans* to justify specific rank.

MALE. The type specimen may be redescribed as follows: Length 6 mm. Body elongate and narrow. First pair of coxal plates narrow with an obtusely pointed tip; the posterior margin possesses a row of about six setae with a single seta on the middle of the margin the origin of which is not marked by a tooth; dorsally there is a row of about eight setae on the outer face. Coxal plates II, III and IV deeper than the corresponding segments. Second pair of coxal plates triangular in outline with a pronounced tooth posteriorly defined by a deep sulcus, and carrying a row of about twenty-one bristles ventrally. Third pair of coxal plates rectangular in outline, otherwise as the second pair. Last pair of epimeral plates (pleon segment III) evenly rounded at the posterior corner without any trace of a tooth; the lower edge carries numerous groups of spines with one to three spines per group, reading 2.2.3.1.2.2.2.1.1.1, the posterior edge with three hairs. Pleon segment IV deeply depressed dorsally with a pair of anteriorly directed bristles and a pair of posteriorly directed spines; an additional pair of spines may be present in some specimens. The basal joint of the antennule is produced into a triangular point (N.B. "Angulus capitis acutus productus"), lower border with five feathered hairs. Flagellum of eleven joints of which the first nine carry calceoli and a dense tuft of aesthetascs. Accessory flagellum long and narrow with the second joint a little less than a third the length of the basal, as 31 : 100; the basal carries four groups of spines on the inner margin and a tuft of setae on the outer margin. The flagellum of the antenna is longer than the body. The propodus of the first gnathopod is an oblong oval as in the other species except *elegans*. Peraeopod III with the merus twice as long as broad, as 100 : 50, the relation of the length of the merus to carpus plus propodus combined as 100 : 84, the anterior border carries an edge row of about twenty-six feathered bristles with a row of about twenty-five spines on the outer face. Peraeopods IV and V elongate and narrow, peraeopod V with the carpus longer than the propodus, as 100 : 85, dactylus pointed as a spine. The outer ramus of uropod III is long and narrow with the second joint more than a

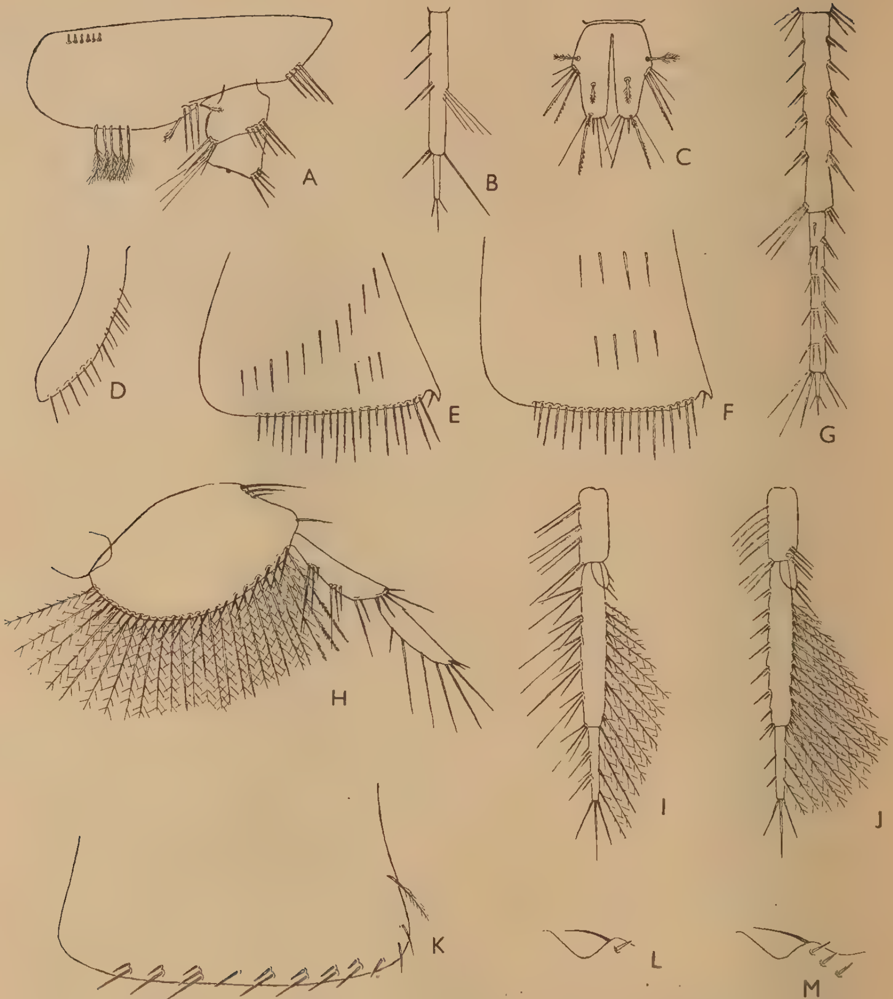


Fig. 4. *B. tenuipes* ♂. *a*, Basal joint of antennule. *b*, Accessory flagellum of antennule. *c*, Telson. *d*, First coxal plate. *e*, Second coxal plate. *f*, Third coxal plate. *g*, Carpus, propodus and dactylus of peraeopod V. *h*, Merus, carpus and propodus of peraeopod III. *i*, Third uropod of ♀. *j*, Third uropod of ♂. *k*, Third epimeral plate. *l*, Fourth pleon segment of type specimen. *m*, Fourth pleon segment of male from unrecorded locality in Kattegat.

third the length of the basal, as 45 : 100; the basal joint carries thirteen and the second joint three feathered bristles on the inner margin, each with an associated short seta; the outer margin with eight groups of spines. Telson with an apical armature of two or three bristles, one spine, one plumose hair, two or three bristles one of which may be modified to a serrated bristle, two bristles, laterally with two serrated bristles, two bristles. Eyes large and reniform. Colour unknown. A comparison of other adult males with the type shows but little variation.

FEMALE. The female differs from the male in the following points: the flagellum of the antennule with six or seven joints, accessory flagellum without a tuft of setae on the outer margin, the second joint from a quarter to more than a third the length of the basal. The flagellum of the antenna with eight to ten joints, the relation of the length of the flagellum to fourth and fifth joints of the peduncle combined as 84 : 100, but somewhat variable. The outer ramus of uropod III with about seven feathered bristles on the inner margin with the accessory bristles well developed, the outer margin with ten groups of well-developed spines, the spines almost as long as the feathered bristles. The anterior border of the merus of peraeopod III carries a greater number of feathered bristles. The ventral margin of the second and third coxal plates a greater number of bristles. The fourth pleon segment is less deeply depressed.

Thus the main points in which *tenuipes* differs from *elegans* are (i) the triangular end to the basal joint of the antennule with four or five feathered hairs on the lower margin, (ii) the well-developed tooth at the posterior corner of coxal plates II and III, (iii) the numerous rows of spines on the third epimeral plates, and (iv) the length of the second joint of the outer ramus of uropod III which is more than a third the length of the basal.

Geographically this species has a wide distribution, but due to its previous confusion with *elegans* the number of records are few. The author has examined the collections of *B. pelagica* of the Copenhagen Museum, which show *tenuipes* as occurring at five stations in the Kattegat; the Stockholm Museum collections contain one tube of this species labelled as from the Kristiniberg Biological Station without exact locality. In the Norman collection in the British Museum there are specimens from Guernsey (register numbers 13782–791 and 13808–812), from Start Bay, Devon (13817–821), from the Kattegat (13859), from the Scilly Isles (13875) and from two stations of the *Porcupine* Expedition, 1869, namely St. 6, west of the Shannon, Ireland, 90 fathoms (13871–874), and St. 18, west of Clew Bay, Ireland, 183 fathoms (13856–858). Crawford (1937*a*, p. 639) records it as *B. elegans* (see footnote, p. 222) from Cawsand Bay, Plymouth.

B. gracilis Sars (Fig. 1, *h–m*)

This is a somewhat doubtful species described by Sars (1891, p. 132, pl. 45, f. 1) from an adult male and female collected from comparatively deep water off the Norwegian coast. The male specimen only is extant.

An examination of the male specimen shows that it agrees in certain features with *tenuipes*, to which it seems most nearly related. It agrees with *tenuipes* in possessing (i) a well-developed tooth at the posterior corner of coxal plates II and III; the shape of the first coxal plate was not ascertained, but Sars describes it as obtusely pointed. (ii) Peraeopods IV and V are long and narrow, (iii) the third epimeral plate is evenly rounded at the posterior corners and carries numerous groups of spines, (iv) the pleon segment IV carries more than one pair of backwardly directed spines. (v) The third uropod is missing in the specimen, but Sars' drawing of this appendage in the female shows its agreement with *tenuipes*. It differs from *tenuipes* in (i) the rounded end to the basal joint of the antennule with two feathered hairs on the lower margin; (ii) the second joint of the accessory flagellum is short and about a fifth the length of the basal; (iii) the merus of peraeopod III is not expanded, it is more than twice as long as broad. It is unlike any other species in the character of the flagellum of the antenna in the male, which is short and composed of thirteen joints of which the first five carry calceoli. It seems advisable to retain this species until further specimens are available.

B. pilosa Lindström (Fig. 5)

B. pilosa Lindström, 1855, p. 59, pl. 2, f. 1–11; Sars, 1891, p. 133, pl. 45, f. 2; Stebbing, 1906, p. 121; Stephensen, 1928, p. 132, f. 25.
B. robertsoni Bate, 1862, p. 173, pl. 31, f. 5; Bate & Westwood, 1863, p. 307.

Type specimen, a female, not extant. Locality, off the island of Gottland, Baltic. A brief description of specimens collected at Kames Bay, Millport, which have been compared with specimens from the Baltic kindly loaned by Dr Sixten Bock of the Zoological Museum, Stockholm, follows:

MALE. Length not exceeding 6 mm. Body robust. First pair of coxal plates with a pointed tip and with a group of three or four bristles on the posterior margin; the origin of a single bristle dorsal to this group is not marked by a tooth. Coxal plates II, III and IV are not as deep as the corresponding segments and thus are smaller than in the other species. Second pair of coxal plates rounded but narrowing towards the base; the ventral margin carries a row of about five to six bristles and the posterior corner is not marked by a tooth. Third pair of coxal plates rectangular, but narrowing towards the base, otherwise as the second pair. Last pair of epimeral plates (pleon segment III) evenly rounded at the posterior corner without any trace of a tooth; the number of groups of spines is less than in the other species, a typical arrangement is 2.1 or 3.1. Pleon segment IV deeply depressed dorsally with a pair of anteriorly directed bristles. The basal joint of the antennule is evenly rounded at the tip which is narrower than in the other species; lower margin with two feathered hairs; the number of joints in the flagellum varies from ten to fourteen of which the first eight to twelve carry calceoli and a small group of three to four aesthetascs, the flagellum is longer than in the other

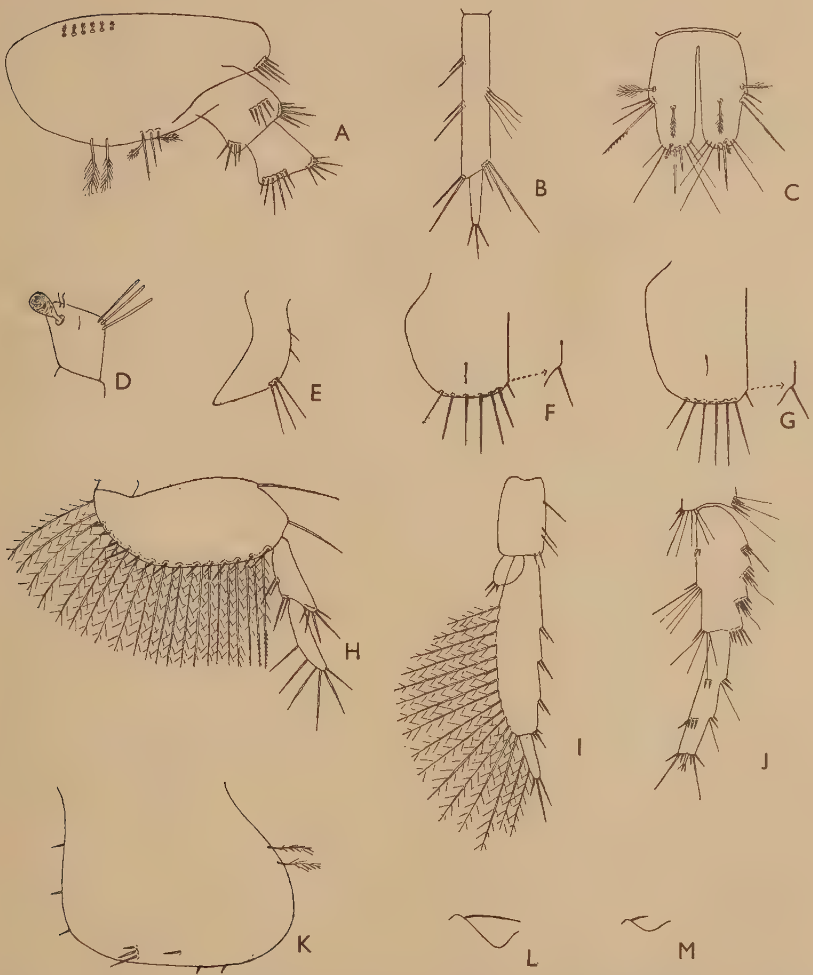


Fig. 5. *B. pilosa* ♂. *a*, Basal joint of antennule. *b*, Accessory flagellum of antennule. *c*, Telson. *d*, Typical joint from middle of flagellum of antennule. *e*, First coxal plate. *f*, Second coxal plate. *g*, Third coxal plate. *h*, Merus, carpus and propodus of peraeopod III. *i*, Third uropod. *j*, Carpus, propodus and dactylus of peraeopod V. *k*, Third epimeral plate. *l*, Fourth pleon segment in ♂. *m*, Fourth pleon segment in ♀.

species and the number of aesthetascs fewer. Accessory flagellum with the second joint less than a third the length of the basal, as 29 : 100, with three groups of spines on the inner margin and a tuft of setae on the outer margin. The flagellum of the antenna is about one-half to two-thirds the length of the body, the number of joints varying from seventeen to over thirty, all of which apart from the last one or two carry calceoli. The propodus of the first gnathopod as in the other species except *elegans*. The merus of peraeopod III is more than twice as long as broad, as 100 : 46; its anterior margin carries a row of from eighteen to twenty-four feathered bristles, and is much longer than the carpus plus propodus combined, as 100 : 71. The carpus and propodus of peraeopod V are of equal length, the carpus is broad and more robust than in the other species. The basal joint of the outer ramus of the third uropod is expended along the middle of its length, with from twelve to eighteen feathered bristles on the inner margin and three to four groups of spines on the outer margin; the second joint is less than a third the length of the basal as 26 : 100, with one to three feathered bristles on its inner margin. A typical arrangement of the armature at the apex of the telson is, reading from within outwards, two or three bristles, two spines, one plumose hair which may be absent, two to four bristles, the inner one of which may be modified to a serrated bristle, laterally one serrated bristle and two bristles. Eyes reniform with dark red pigment.

FEMALE. The female differs from the male in the following points: the flagellum of the antennule with six or seven joints, accessory flagellum without a tuft of setae on the outer margin and with the second joint on an average more than a third the length of the basal, as 37 : 100. The flagellum of the antenna with eight or nine joints and in length less than the fourth and fifth joints of the peduncle combined, as 83 : 100. The number of feathered bristles on the anterior border of peraeopod III varies from twenty-three to thirty, on the inner margin of the third uropod from five to ten. The number of groups of spines and spines per group on the third epimeral plate of ten specimens gave the following readings: 1 (twice), 1.1 (twice), 1.1.1, 2.1 (four), 2.1.1. Eyes round with dark red pigment. Eggs blue.

Colour of body variable; in the reddish sands of Kames Bay the amount of red pigment in the pleon is considerable, in the lighter coloured sands of the Welsh coast pigment it is much less.

Geographically this species occurs in numerous localities in the Baltic from the Danish coast to the island of Gottland (Oldevig, 1933), in the Kattegat and on the North Sea coast of Denmark (specimens in the Zoological Museum, Copenhagen), in the Oslo fjord (specimens in the Zoological Museum, Oslo). My only records of it from the east coast of England and Scotland are Leigh-on-Sea (Essex) collected by Crawford (specimens in the British Museum) and from Amble (Northumberland), specimens supplied by Professor A. D. Hobson, Newcastle, who also collected it in the Hebrides in 1937. Further collecting in the estuaries on the east coast will probably add many records.

I have no records from the English Channel. On the west coast of Britain it is abundant in several localities. I have collected it in the estuaries and sandy beaches of the west coast of Wales, at Kames Bay, Millport, and on the Ayrshire coast; in these localities it occurs above the high-water mark of neap tides, occasionally in water of somewhat reduced salinity. Crawford (1937*b*, p. 652) records it as *Bathyporeia* sp. from the River Taw, North Devon.

B. sarsi, nom.nov. (Fig. 6)

B. robertsoni Sars, 1891, p. 131, pl. 44, f. 2; Scott, 1893, p. 213, pl. 5, f. 26–9; Stebbing, 1906, p. 121; Chevreux & Fage, 1925, p. 94, Stephensen, 1928, p. 132, f. 25.
B. pilosa Elmhirst, 1931, p. 170.

Type specimens, three adult males, two of which are extant, in the Zoological Museum, Oslo. Locality (Sars, 1891, p. 132) Sorvaer, west coast of Finmark, northern Norway.

The specimens described by Bate as *B. robertsoni* were collected by Robertson on "Cumbrae...in sand pools, near low water mark, numerous darting hither and thither". Bate gave two somewhat meagre descriptions and two contradictory drawings of these specimens, the first (1862, p. 173, pl. 31, f. 5) shows fourteen joints in the flagellum of the antennule and twenty-four joints with calceoli in the flagellum of the antenna; the second (1863, p. 307, with figure) shows ten joints in the flagellum of the antennule and eighteen joints in the flagellum of the antenna. Sars in his description of the Norwegian specimens states "inferior antennae...composed of seventeen articulations each except the last two bearing calceoli". Thus Sars seems to have based his identification of the Norwegian specimens on the second of Bate's drawings. An examination of the type locality of *B. robertsoni* Bate during April 1936, 1937 (Watkin, 1937) and 1938 failed to show a single specimen of this species as described by Sars, but *B. pilosa* Lindström was abundant and an occasional specimen was found with as few as seventeen calceoli-bearing joints in the flagellum of the antenna.

I am myself confident that the *robertsoni* of Bate was *pilosa*, and it thus follows that Sars was dealing with a new species which is here named "sarsi" in compliment to him. The following description is based partly on the two type specimens and partly on specimens from other localities.

MALE. Length not exceeding 6 mm. Body robust. First pair of coxal plates with a rounded tip, the posterior margin with a row of three to four bristles; the origin of a single bristle dorsal to this row is not marked by a tooth. Coxal plates II, III and IV as deep as the corresponding segments. Second pair of coxal plates square in outline with about four to five bristles on the ventral margin; the posterior corner is not marked by a tooth but a definite ridge may occur in some specimens. Third pair of coxal plates rectangular in outline, otherwise much as the second pair. Last pair of epimeral plates (pleon segment III) with the posterior corner rounded, the lower edge

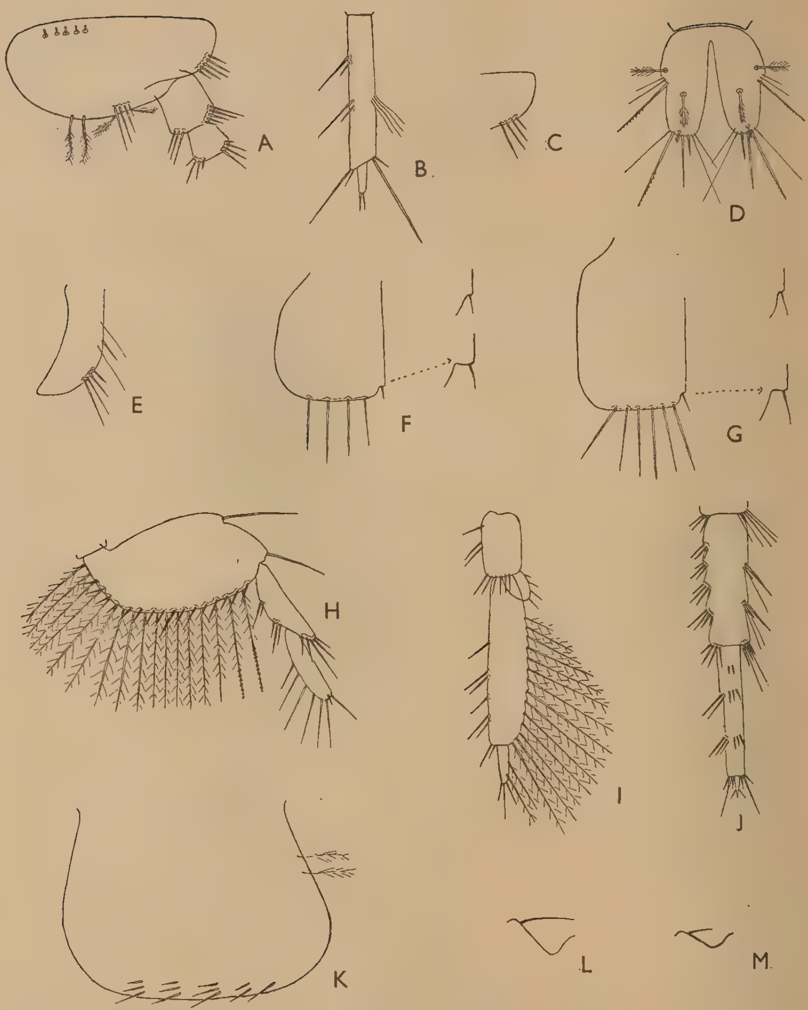


Fig. 6. *B. sarsi* ♂. *a*, Basal joint of antennule. *b*, accessory flagellum of antennule. *c*, Apex of basal joint of antennule in ♀. *d*, Telson. *e*, First coxal plate. *f*, Second coxal plate. *g*, Third coxal plate. *h*, Merus, carpus and propodus of peraeopod III. *i*, third uropod. *j*, Carpus, propodus and dactylus of peraeopod V. *k*, Third epimeral plate. *l*, Fourth pleon segment in ♂. *m*, Fourth pleon segment in ♀.

carried four to five groups of spines, typical arrangements are 3.3.3.2.1, or 3.3.2.1. Pleon segment IV deeply depressed dorsally with a pair of anteriorly curved bristles only. The basal joint of the antennule with an evenly rounded tip, with two or three plumose hairs ventrally; the flagellum is of ten or eleven joints of which the first eight or nine carry calceoli and a dense tuft of aesthetascs. The accessory flagellum with the second joint less than a fifth the length of the first, as 19 : 100, with three or four groups of spines on the inner border and a tuft of setae on the outer border. The flagellum of the antenna is shorter than in any other species, not exceeding one-half the length of the body, and is composed of fifteen to twenty-two joints each of which carries a calceolus with one or two joints without a calceolus. Eyes reniform. Colour unknown.

The propodus of the first gnathopod a rounded oval as in the other species except *elegans*. The merus of peraeopod III is about twice as long as broad, as 100 : 51, the anterior border with seventeen to twenty-two feathered bristles. Peraeopod V with the propodus longer than the carpus, as 100 : 90, dactylus pointed as a spine. The second joint of the outer ramus of the third uropod is about a quarter the length of the basal, as 24 : 100, the basal joint is expanded along the middle of its length with twelve to sixteen feathered bristles on the inner margin and four groups of spines on the outer margin, second joint with two to three feathered bristles. A typical arrangement of the armature at the apex of the telson is as follows, reading from within outwards: two or three bristles, two spines, one plumose hair, one or two bristles the inner of which may be modified as a serrated bristle; laterally one serrated bristle, one or two bristles.

FEMALE. The female differs from the male in the following points: Length 7–8 mm. The basal joint of the antennule has a more square tip; the number of joints in the flagellum is seven or eight; accessory flagellum without a tuft of setae on the outer margin of the basal joint. The number of joints in the flagellum of the antenna is eight to ten, the relation of its length to the fourth and fifth joints of the peduncle being as 78 : 100. The second and third coxal plates carry numerous bristles on their ventral margins, the number increasing with age up to about twenty-four. The anterior margin of the merus of peraeopod III carries many more feathered bristles: counts of up to forty were recorded. The number of groups of spines on the third epimeral plate is greater, a typical arrangement is 3.3.2.2.1.1. The number of feathered bristles on the inner margin of the outer ramus of the third uropod is less, varying from ten to fourteen. Pleon segment IV is less deeply depressed.

Geographically this species occurs along the whole of the Norwegian and Danish coasts, on the French and English sides of the English Channel, and in several localities along the east coast of Scotland and England. Its absence from the west coast of Britain is peculiar, but extensive collecting failed to record its occurrence. It is usually an intertidal or shallow water form.

B. lindströmi Stebbing

B. lindströmi Stebbing, 1906, p. 122.
B. pilosa (part), Della Valle, 1893, p. 752, pl. 5, f. 1; pl. 36, f. 19–32.

Della Valle referred *pelagica*, *robertsoni* and *gracilis* to the synonymy of *pilosa*, and described and figured specimens collected from sand in the Bay of Naples at a depth of 10–20 m. as *pilosa*. Stebbing formed the doubtful species *lindströmi* on the description and figures of *pilosa* as given by Della Valle. This form is obviously different from *pilosa* and *sarsi* in that the coxal plates are toothed and the fourth pleon segment carries a pair of backwardly directed spines. The third epimeral plate is rounded at the posterior corner, and thus it may agree with *elegans*, *tenuipes* or *gracilis*, but the description and figures are insufficient for correct determination. The absence of the dactylus in peraeopod V and the lack of armature at the apex of the telson are probably incorrect. The original specimens described by Della Valle are lost and no further specimens are at the moment available. The Norman collection in the British Museum contains two tubes labelled as from Naples, but the specimens are somewhat damaged and brittle and unreliable for detailed description. This species must remain a doubtful one until further specimens are available. It is omitted from the key given below.

Key to the Identification of the Species

1. Fourth segment of pleon with spines directed posteriorly and bristles anteriorly 2
Fourth segment of pleon with anteriorly directed bristles only ... 5

2. Third epimeral plate, in adult females and young males, with tooth at or near the posterior corner. In adult males the tooth is reduced, its reduction being indicated by an uneven border... 3
Third epimeral plate evenly rounded at posterior corner 4

3. Third epimeral plate with well-developed tooth at posterior corner which extends beyond the vertical margin of the posterior border (reduced in adult males). Second and third coxal plates with tooth at posterior corner ... ... *guilliamsoniana*
Third epimeral plate with small tooth almost at the posterior corner, not extending beyond the vertical margin of posterior border (reduced in adult males). Second and third coxal plates without tooth at posterior corner ... ... *pelagica*

4. Basal joint of the antennule rounded at tip; coxal plates II and III with small tooth on posterior corner... ... ... *elegans*
Basal joint of the antennule produced to a point; coxal plates II and III with well-developed tooth at posterior corner ... *tenuipes*
Basal joint of the antennule rounded at the tip; coxal plates II and III with well-developed tooth at posterior corner ... ... *gracilis*

5. Third epimeral plate with not more than three groups of spines; basal joint of antennule with a rounded but narrow tip ... ... *pilosa*
   Third epimeral plate with from four to six groups of spines; basal joint of antennule with a rounded but broad tip ... ... *sarsi*

ACKNOWLEDGEMENTS

The author desires to acknowledge his indebtedness to Dr K. Stephensen, Dr Sixten Bock and Dr Johan Huus, of the Zoological Museums of Copenhagen, Stockholm and Oslo respectively, for forwarding their collections of the species in this genus for examination; to Dr I. Gordon, of the British Museum, for permission to examine the Spence Bate and Norman collections; to Dr S. Kemp, of the Marine Biological Association, for the loan of the Plymouth collections; to Professor A. D. Hobson, Newcastle, for the loan of specimens from the North East coast and the Hebrides; to Mr G. I. Crawford, of the British Museum, for specimens from the Hampshire coast and information regarding his collections of this genus.

This work was in part carried out at the Laboratory of the Scottish Marine Biological Station, Millport, and my thanks are due to the Director, Mr R. Elmhirst, for facilities afforded me there in collecting specimens and for permission to examine the Robertson collection and the numerous tubes of specimens from many localities around the Scottish coast. Finally, I have to thank Professor R. D. Laurie for his interest in the progress of this research which was undertaken mainly in the Department of Zoology, University College of Wales, Aberystwyth.

REFERENCES

BATE, C. SPENCE, 1856. On the British Edriophthalma. *Rep. Brit. Ass. Meet.*, 1855, p. 59.

—— 1857*a*. A synopsis of the British edriophthalmous Crustacea. Pt. I. Amphipoda. *Ann. Nat. Hist.*, Vol. XIX, Series 2, p. 146.

—— 1857*b*. British Amphipoda. *Ann. Nat. Hist.*, Vol. XIX, Series 2, p. 271.

—— 1862. *Catalogue of Amphipodous Crustacea*, British Museum, pp. 172–4.

BATE, C. SPENCE & WESTWOOD, J. O., 1863. *A History of British Sessile-Eyed Crustacea*, Vol. I, pp. 304–10.

BLANC, H., 1884. Die Amphipoden der Kieler Bucht. *Deutschen Akad. der Naturforscher*, Band XLVII, No. 2.

CHEVREUX, E., 1887. Catalogue des Crustacés Amphipodes marins du Sud-Ouest de la Bretagne. *Ext. de Bull. de la Soc. Zool. de France*, t. XII.

CHEVREUX, E. & FAGE, L., 1925. Amphipodes. *Faune de France*, Vol. 9, pp. 91–5.

CRAWFORD, G. I., 1937*a*. Notes on the distribution of burrowing Isopoda and Amphipoda in various soils on the sea bottom near Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 635–9.

—— 1937*b*. The fauna of certain estuaries in west England and south Wales, with special reference to Tanaidacea, Isopoda and Amphipoda. *Journ. Mar. Biol. Assoc.*, Vol. XXI, p. 652.

DELLA VALLE, A., 1893. Gammarini del Golfo di Napoli. *Fauna und Flora des Golfes von Neapel*, Vol. 20, pp. 751–4.

ELMHIRST, R., 1931. Studies on the Scottish marine fauna. The Crustacea of the sandy and muddy areas of the tidal zone. *Proc. Roy. Soc. Edinb.*, Vol. LI, Pt. 2, No. 21, pp. 169–71.

LINDSTRÖM, G., 1855. Bidrag till kannedomen om Osterjons invertebrate-fauna. *Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar*, Arg. 12, No. 2, p. 59.

MEINERT, F. V. A., 1877. Crustacea, Isopoda, Amphipoda et Decapoda Daniae. *Naturhistorisk Tidsskrift*. III. Raekkes, II. Band, p. 201.

MOORE, H. B., 1937. Marine fauna of the Isle of Man. *Proc. and Trans. Liverpool Biol. Soc.*, Vol. L, p. 118.

NORMAN, A. M., 1900. British Amphipoda, families Pontoporeidae to Ampeliscidae. *Ann. Nat. Hist.*, Vol. V, Series 7, p. 326.

—— 1905. Revised nomenclature of Bate & Westwood's sessile-eyed Crustacea. *Ann. Nat. Hist.*, Vol. XVI, p. 82.

OLDEVIG, H., 1933. Sveriges Amphipoder. *Meddel. fran Gotebergs Musei Zool.* No. 62.

RAITT, D. S., 1937. The benthic Amphipoda of the north-western North Sea and adjacent waters. *Proc. Roy. Soc. Edinb.*, Vol. LVII, p. 249.

SARS, G. O., 1891. *An Account of the Crustacea of Norway*, Vol. I, *Amphipoda*, pp. 127–34.

SCOTT, T., 1893. Additions to the fauna of the Firth of Forth, Pt. V. *Eleventh Ann. Rep. Fish. Bd. for Scotland*, p. 213.

SEXTON, E. L., 1925. The moulting and growth stages of *Gammarus* with descriptions of the normals and intersexes of *Gammarus chevreuxi*. *Journ. Mar. Biol. Assoc.*, Vol. XIII, pp. 358–60.

STEBBING, T. R. R., 1875. On the genus *Bathyporeia*. *Ann. Nat. Hist.*, Vol. XV, Series 4, p. 74.

—— 1906. Amphipoder. I. Gammaridea. *Das Tierreich.*, Leif. 21, pp. 119–22.

STEPHENSEN, K., 1926. Revideret Fortegnelse over Danmarks Arter af Amphipoda. *Vidensk. Medd. fra Dansknaturh. Foren.*, Bd. 82, pp. 52–5.

—— 1928. *Danmarks Fauna. Tanglopper (Amphipoder)*, pp. 129–32.

WALKER, A. O., 1895*a*. The Amphipoda of Bate & Westwood's British sessile-eyed Crustacea. *Ann. Nat. Hist.*, Vol. XV, Series 6, p. 470.

—— 1895*b*. Revision of the Amphipoda of the L.M.B.C. District. *Trans. Liverpool Biol. Soc.*, Vol. IX, p. 295.

WATKIN, E. E., 1937. The amphipod genus *Bathyporeia*. Note in *Ann. Rep. Scot. Mar. Biol. Assoc. for* 1936–37.

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

ON THE CILIARY MECHANISMS AND INTERRELATIONSHIPS OF LAMELLIBRANCHS

PART II. SORTING DEVICES ON THE GILLS

By D. Atkins

Quart. Journ. Micr. Sci., Vol. 79, 1937, *pp.* 339–73

The following mechanisms are described: (1) Utilization of plicae for sorting in two ways, (*a*) the frontal currents are in opposite directions in the grooves and on the crests, and particles intended for consumption are carried in the grooves to the safe dorsal channels, e.g. in *Pecten*, (*b*) the plical grooves open into the safe channel at the bottom of the deep marginal groove, while the crests lead to a superficial path along the lobes of the marginal groove, e.g. in *Pinna*. (2) Acceptance and rejection of material by the opening and closing of a deep marginal groove, e.g. in *Solecurtus scopula*. (3) Presence of guarding cilia on the lobes of the marginal groove, preventing the entry of large masses, but allowing that of small particles, e.g. in *Musculus marmoratus*. (4) Presence of cirri (in addition to the usual frontal cilia), which remove grains of sand and rock from the gills, e.g. in *Mactra corallina*, *Barnea parva*.

Small gills and large palps are found in certain deposit feeding bivalves with long free siphons, and forwardly beating cirri on the ends of the gills provide extra help to draw the current down the long inhalent siphon.

Certain of the ciliary structures are clearly adaptive, correlated with feeding difficulties incidental to the habitat. A preliminary sorting of material on the gills, before it is passed on to the palps, is far from unusual in lamellibranchs.

D. A.

ON THE CILIARY MECHANISMS AND INTERRELATIONSHIPS OF LAMELLIBRANCHS

PART III. TYPES OF LAMELLIBRANCH GILLS AND THEIR FOOD CURRENTS

By D. Atkins

Quart. Journ. Micr. Sci., Vol. 79, 1937, *pp.* 375–421

The gills of some ninety odd species (chiefly marine), belonging to sixty genera and forty-one families, have been investigated and grouped under seven main types (with subtypes) according to structure and ciliary currents.

D. A.

ON THE CILIARY MECHANISMS AND INTERRELATIONSHIPS OF LAMELLIBRANCHS

PART IV. CUTICULAR FUSION, WITH SPECIAL REFERENCE TO THE FOURTH APERTURE IN CERTAIN LAMELLIBRANCHS

By **D. Atkins**

Quart. Journ. Micr. Sci., Vol. 79, 1937, *pp.* 423–45

A form of fusion involving only the cuticle has been found between the dorsal edges of the ascending lamellae of the outer demibranchs and the mantle or visceral mass in *Solen marginatus* Montagu, *Ensis siliqua* (L.), *E. arcuatus* (Jeffreys), *Cultellus pellucidus* (Pennant), *Solecurtus scopula* (Turton), *Lutraria lutraria* (L.), and *Tellina tenuis* da Costa; between the dorsal edges of the ascending lamellae of the two inner demibranchs in *Barnea parva* (Pennant); and between the mantle lobes in the mid-ventral line between the pedal and fourth apertures in *Ensis siliqua*, *E. arcuatus* and *Cultellus pellucidus*. A more advanced stage of fusion occurs in this last position in *Lutraria lutraria*. The histological structure of the junction is described, and is especially considered in relation to the condition of the fourth aperture in the Solenidae.

D. A.

CHOLINESTERASE IN INVERTEBRATE MUSCLES

By **Z. M. Bacq** and **D. Nachmansohn**

Journal of Physiology, Vol. 89, *No.* 4, 1937, *p.* 368

The rate of hydrolysis of acetylcholine by muscle is the same in crustaceans (*Homarus vulgaris*), molluscs (*Eusepia officinalis*) and echinoderms (*Holothuria nigra*). The hydrolysis by the muscle of a sea-leech is apparently a little slower.

Cholinesterase is absent from the sphincter muscle of the sea-anemone.

The hydrolysis of acetylcholine by the brain ganglion of *Eusepia* is more than ten times quicker than by muscle.

Z. M. B.

STUDIES IN TUNICATE DEVELOPMENT. III

DIFFERENTIAL RETARDATION AND ACCELERATION

By **N. J. Berrill**

Phil. Trans. Roy. Soc. B, Vol. 225, 1935, *pp.* 255–326

The development of forty-four species was investigated. The rate of cleavage, gastrulation and of differentiation of larval tissues varies directly with the (volume)/(free surface-area) of the egg and embryo. Cell division ceases at an early stage in the larval structures, cell numbers remaining constant, cell sizes varying with the egg volume. In the permanent organs and tissues cell division continues until a minimal size is reached, so that cell numbers vary with the egg volume.

An increase in proportion of yolk to cytoplasm retards the rate of development up to and including gastrulation. After gastrulation cell division in tadpole tissues has in any case ceased and differentiation is in progress. The rate of this differentiation is retarded to the same degree as early development. But the rate of cleavage and development of permanent tissues becomes progressively accelerated.

Increase in egg volume or increase in proportion of yolk to cytoplasm induces a telescoping of development. The development of larval chordate (tadpole) structure and that of the permanent ascidian structure are virtually independent of one another. N. J. B.

STUDIES IN TUNICATE DEVELOPMENT. IV

By N. J. Berrill

Phil. Trans. Roy. Soc. B, Vol. 225, 1935, *pp.* 327–79

An investigation of budding in *Diazona*, *Tylobranchion*, *Morchellium*, *Enherdmania*, *Endistoma*, *Archidistoma*, *Pycnoclavella*, *Chondrostachys*, *Distaplia*, *Colella*, *Clavelina*, *Diplosoma*, *Perophora*, *Ecteinascidia*, *Stolonica*, *Distomus*, *Polyandrocarpa*, *Symplegina*, *Botryllus* and *Botrylloides*.

Budding is usually correlated with autolysis or antero-posterior regression of the zooid. Regression results from the migration posteriorly of yolk-laden trophocytes. The extent of the migration depends upon the nature of the zooid. Where there is no post-abdomen nor enlarged ventral vessel, the abdomen regresses. Where the ventral vessel is enlarged it becomes congested, forming the buds and allowing the rest of the zooid to regress. Isolation of buds is effected by transverse epidermal constriction. The tissues within the bud depend upon the region constricted by the epidermis. When part of the digestive tube persists, bud development is primarily a regeneration, when absent, a reorganization. Highly specialized tissue can survive but is unable to proliferate. Moderately specialized tissue can proliferate to form more of its own kind but no other. Unspecialized tissues, such as epicardial, septal, or atrial, alone are multipotent. The vascular septum of the ventral stolon has no connexion at any time with the epicardium and cannot be considered as an extension of the epicardium into the stolon for purposes of budding.

N. J. B.

STUDIES IN TUNICATE DEVELOPMENT. V.

THE EVOLUTION AND CLASSIFICATION OF ASCIDIANS

By N. J. Berrill

Phil. Trans. Roy. Soc. B, Vol. 226, 1936, *pp.* 43–70

The morphology and development of the heart and epicardium is described of *Ciona*, *Diazona*, *Phopalea*, *Tylobranchion*, *Enherdmania*, *Sidnyum*, *Endistoma*, *Archidistoma*, *Distaplia*, *Colella*, *Diplosoma*, *Pycnoclavella*, *Clavelina*, *Perophora*, *Ecteinascidia*, *Ascidia* and *Molgula*. A new classification of the Ascidiacea is proposed, based on the nature of the epicardium. The function of the epicardium is found in its most primitive condition in *Ciona*, where it is of a coelomic nature. The importance of the epicardium in the budding stolons of *Diplosoma*, *Aplidium* and the Thaliacea, and as an excretory organ in the Ascidiidae, Styclidae, Pyuridae, and Molgulidae is the result of extreme specialization in different directions of functions present, though poorly developed, in *Ciona*.

N. J. B.

CELL DIVISION AND DIFFERENTIATION IN ASEXUAL AND SEXUAL DEVELOPMENT

By N. J. Berrill

Journ. Morph., Vol. 57, 1935, *pp.* 353–427

In ascidians the development of eggs and of buds are in sharp contrast. In bud development cell sizes are minimal throughout. Gross differentiation of form becomes apparent from the beginning, histological differentiation only when cell division is ending. The position of a cell relative to the whole determines its nature. Multiplication of cells continues until sufficient have been formed for the expression of all specific and other characters. In sexual development the egg is a large cell which divides until the minimal cell sizes characteristic of the species are obtained. The course of cleavage is a curve suggesting the attainment of a state of equilibrium. Commencing before fertilization and continuing during cleavage is a precocious differentiation of certain parts that inhibits further cell division and results in the formation of special larval structures that function when a mere fraction of the whole developmental period has elapsed. This differentiation may be suppressed, or may be retarded, without affecting the development of the rest of the egg. In the remaining parts cell division continues until minimal cell sizes are reached, and only then does histological differentiation become apparent, as in sexual development. The number of cells thus formed is very small compared with that necessary for the expression of the full character of the species, and the newly functional post-larval organism is necessarily peculiar in structure.

N. J. B.

REGENERATION IN *CLAVELINA LEPODIFORMIS*

By N. J. Berrill and A. Cohen

Journ. Exp. Biol., Vol. XIII, 1936, *pp.* 352–62

The number of rows of stigmata formed during the development of a stolon fragment varies directly with the size of the fragment. In very small pieces development may become arrested at almost any stage, depending upon the quantity of mesenchyme contained in the proximal region of the stolon piece. If sufficient is present to enable development to proceed to the formation of a functional heart, a circulation is established that includes food reserves in the distal part of the stolon, and development proceeds to completion. In shorter pieces, less than 0·4 mm. long, development or regeneration does not begin. Total failure to develop is correlated with the absence of a region of relatively columnar epidermis. N. J. B.

REORGANIZATION AND REGENERATION IN *SABELLA*. I. NATURE OF GRADIENT, SUMMATION, AND POSTERIOR REORGANIZATION. II. THE INFLUENCE OF TEMPERATURE. III. THE INFLUENCE OF LIGHT

By N. J. Berrill and D. M. Mees

(I) Journ. Exp. Zool., Vol. 73, 1936, *pp.* 67–83. *(II and III) Ibid., Vol.* 74, 1937, *pp.* 61–89

I. When abdominal parapodia are reorganized to form thoracic parapodia during regeneration of a head, a whole thoracic field is imposed at the same time. Failure of regeneration is correlated with a loss of ciliary polarization of original segments. The gradient in time of reorganization of successive segments is due to difference in time of commencement and not to differing rates. Successive decapitations produce a summation of effect. A mixed type of parapodia may appear at the junction of reorganized and normal segments. Posterior thoracic parapodia may appear next to a posterior cut surface. They are to be correlated with a delayed outgrowth of the intestine. Removal of an abdominal parapodium results in the regeneration of a thoracic parapodium.

II. The *rate* of anterior regeneration and that of reorganization have each a temperature coefficient (Q_{10}) of about 2·4. The *range* of reorganization under standard conditions in the dark is about four segments. The range is not affected by temperature, $Q_{10} = 1{\cdot}0$.

III. Light is responsible for reorganization of segments averaging more than four in number. It may increase by twentyfold the number reorganized in the dark. The effective light is within the visible range. It has a threshold intensity of about 15,000 metre-candles below which reorganization is at a minimum. It is most effective during the period of most active morphogenesis, and it acts upon anterior regenerating tissue or tissue adjacent to it.

It is concluded that a photochemical reaction liberates electrical energy rather than a chemical evocator, as a reorganizing force. N. J. B.

The Early Development of Ascidian Eggs

By Arthur Cohen and N. J. Berrill

Biological Bulletin, Vol. 70, 1936, *pp.* 78–88

When unfertilized nude eggs of *Ascidiella aspersa* are stained with Nile Blue it is found that the periphery stains more heavily and is clearly defined from the central region. A tiny peripheral area—the polar pit—remains unstained. Dalcq's statement that the latter is the site of polar body formation could not be confirmed; evidence to the contrary is presented. In the young tadpole the stain becomes confined to the endoderm (gut) and notochord.

Observation on the membraneless nude egg shows that it undergoes a series of changes in shape from the time of polar body formation to first cleavage.

A. C.

A Relation between the Lyotropic Series and Free Energies

By L. H. N. Cooper

Nature, Vol. CXXXIX, 1937, *p.* 284

A relationship is traced between the lyotropic series of anions, which summarizes their behaviour in many physico-chemical reactions, with their free energies of formation.

The position in the series of ions less commonly investigated is forecast together with the probable value for the free energy of formation of the thiocyanate ion. It is suggested that a more quantitative examination of the series from the thermodynamic standpoint may lead to results of value.

L. H. N. C.

Some Conditions Governing the Solubility of Iron

By L. H. N. Cooper

Proc. Roy. Soc., Ser. B, Vol. 124, 1937, *pp.* 299–307.

Since experiment had shown that the amount of ionic iron in true solution in sea water is extremely small, theoretical methods were invoked to calculate the maximum activities of the ions, Fe^{++}, $FeOH^{++}$ and Fe^{+++}, which can exist in sea water at equilibrium. The activity of ferrous ion is controlled by that of ferric ion and by the oxidation-reduction potential of the water, reversible or irreversible. Maximum activities, expressed as mg.-atom/m.^{3} Fe, may be summarized:

			$a_{Fe^{++}}$	
pH	$a_{Fe^{+++}}$	$a_{FeOH^{++}}$	Governed by $a_{Fe^{+++}}$ and reversible oxygen potential	Governed by $a_{Fe^{+++}}$ and irreversible oxygen potential
8·5	4×10^{-16}	5×10^{-10}	2×10^{-15}	1×10^{-10}
8·0	$1{\cdot}3 \times 10^{-14}$	5×10^{-9}	2×10^{-14}	$1{\cdot}5 \times 10^{-9}$
6·0	$1{\cdot}3 \times 10^{-8}$	5×10^{-5}	2×10^{-10}	4×10^{-5}

These amounts are all far less than could be detected by the most delicate methods of analysis. Other tables and equations show the effect on the iron system of change in pH and oxidation-reduction potential. The results are applicable to all natural waters and to many physiological fluids where equilibrium is attained. L. H. N. C.

ON THE FEEDING MECHANISM OF *APSEUDES TALPA*, AND THE EVOLUTION OF THE PERACARIDAN FEEDING MECHANISMS

By Ralph Dennell

Trans. Roy. Soc. Edin., Vol. LIX, *Pt. I, No.* 2, 1937, *pp.* 57–78

The respiratory current of *Apseudes* is produced mainly by the movements of the pedunculate hemispherical epipodite, which closely invests the rounded and swollen base of the second thoracic limb. The oscillation of the epipodite is effected by the alternate action of the peduncular muscles and fluid pressure within the peduncle. Movements of the second and third thoracic limb exopodite produce currents assisting the respiratory current.

An anterior membranous flap on the epipodite margin controls the filter exit—the lateral gap between maxillule and maxilla—and enables the epipodite to draw a current of water—the filter current—through the filter chamber. The maxilla is thus a passive filter. It bears typical filtratory setae, but the maxillipedal brushing setae are prevented from scraping them effectively by a second row of stouter maxillary setae. True maxillary filter-feeding is therefore of little importance. In addition to raptatory feeding, food particles are retained directly by the maxillipedal brushing setae.

The feeding of *Apseudes* is compared with that of other Peracarida, and the functional evolution of the peracaridan feeding mechanisms is discussed.

R. D.

THE ACTION OF A SINGLE VAGAL VOLLEY ON THE HEART OF THE EEL AND THE TURTLE

By Ernst Fischer

Amer. Journ. Physiol., Vol. 117, 1936, *p.* 596

The chronotropic effect of a single vagal volley is markedly dependent on the cycle phase at which the volley reaches the pacemaker. The experimental results can be explained by the assumption that around the pacemaker there are two mechanisms of liberation of an acetylcholine-like substance (A.C.): a quick mechanism with a short latent period, and a slow mechanism with a long latent period. Vagal fatigue or small doses of atropine depress the quick chronotropic A.C. liberation process more than the slow one. Neither the dromotropic nor the inotropic vagal action is dependent on the cycle phase.

Eserine and acetylcholine act more strongly on the inotropic and dromotropic mechanism than on the chronotropic. The results are interpreted as indicating that the different vagal fibres affecting the heart are not only functionally distinct, but that there exist several chemical transmitters for the vagal action.

E. F.

The Structure and Function of the Alimentary Canal of some Species of Polyplacophora (Mollusca)

By Vera Fretter

Proc. Roy. Soc. Edin., Vol. LIX, 1937, *pp.* 119–64

The anatomy and histology of the alimentary canal of *Lepidochitona cinereus* are described in detail and compared with that of *Acanthochitona crinitus*, *Ischnochiton magdalenensis* and *Cryptochiton stelleri*. All agree in the most important points. The physiology of the gut is studied in *Lepidochitona cinereus* and *Acanthochitona crinitus*.

The buccal cavity containing the odontophore, the openings of a pair of salivary glands and the subradular sac, leads into the oesophagus which expands laterally into a pair of anterior pouches and receives the ducts of a pair of posterior pouches or "sugar glands". The "sugar glands" secrete a diastatic enzyme which passes with the food into the stomach, where it is also mixed with a proteolytic enzyme secreted by the digestive gland. The products of digestion and the undigested food are passed into the anterior intestine whence the soluble products are squeezed into the liver ducts by the action of an intestinal valve or sphincter. The valve regulates the passage of food through the gut and also shapes the oval faecal pellets, which are further moulded and coated with secretion from the gland cells in the extensive coils of the posterior intestine.

Structurally the alimentary canal shows remarkable similarity to that of the lower gastropods.

V. F.

I. Amphipoda. II. Decapod Larvae from Newfoundland Waters

By Nancy Frost

Reps. Faunistic Series No. 1, *Div. Fish. Res. Nfld.*, 1936

The Amphipoda and decapod larvae collected in Newfoundland waters during the period beginning fall 1931 and ending fall 1935 are listed. Of the twenty-eight species of Amphipoda, eight belong to the Hyperidea and twenty to the Gammaridea. Of the latter, one is a new species of the genus *Hippomedon*. This is described and figured.

Decapod larvae of sixteen species are recorded with detailed descriptions where necessary. The most common were found to belong to the genera

Pandalus, *Spirontocaris*, and *Hyas*. Of these the megalopa attributed to *Hyas araneus* (Linn.), apparently, has not been described before. Among the less common decapod larvae are species belonging to the genera *Caridion*, *Pontophilus*, *Sabinea*, *Cancer* and *Latreillia*. In addition a description is given for the first time of a young stage of *Latreutes fucorum* Stimpson. N. F.

The Life History of some Marine Plankton Diatoms

By F. Gross

Phil. Trans. Roy. Soc. B, Vol. 228, 1937, *pp.* 1–47

The observations and experiments described were made on cultures of *Ditylum Brightwelli* and several other species.

Mitosis was found to be very similar to that of other algae. Resting spores occurred regularly in *Ditylum* cultures during autumn, winter and early spring, not in summer. They are spherical bodies formed inside the parental shell by contraction of the protoplast.

The interaction of three factors was found to cause the formation of resting spores: (1) changes of the medium due to crowding; (2) low temperature; (3) low light intensity. Before the density of the cultures reaches such a degree that persistent resting spores are formed, their formation takes place for some time overnight, followed by germination in the course of the next day. The process of germination is described.

A continuous decrease of the average cell diameter could be established in all the species investigated. When the diameter of the diatoms reaches a certain minimum size no further division is possible and they perish unless they form auxospores which develop into big cells. Formation and development of auxospores are described. It only takes place in diatoms of a certain diameter, and may be induced by environmental factors.

Cytological observations support the view that reduction division and an autogamic sexual process precede auxospore formation. No microspores take part in this process. F. G.

The Nerve Net of the Actinozoa. V. Temperature and Facilitation in *Metridium senile*

By D. M. Hall and C. F. A. Pantin

Journ. Exp. Biol., Vol. xiv, 1937, *pp.* 71–8

The chief protective response of *Metridium* is due to the contraction of the longitudinal mesenteric muscles and not to contraction of the sphincter as in *Calliactis*.

A simple apparatus for electrical stimulation of Actinozoa is described.

As in *Calliactis*, the response to electrical stimulation in *Metridium* does not depend on the intensity of individual shocks but on their number and frequency; moreover, *Metridium* obeys the rule that a stimulus produces no effect. As in *Calliactis*, graded responses can be produced in *Metridium* by varying the frequency of stimulation. The longitudinal mesenterics require the highest frequency for a facilitated response, the parietals require a lower frequency and the sphincter requires a relatively high frequency but its action is delayed owing to its slow rate of contraction. The graded responses of different muscles to stimulation are controlled by facilitation; they are not connected with differences in threshold.

Both contraction and relaxation of *Metridium* are slowed at low temperatures ($Q_{10}=2$). The facilitating effect of a stimulus endures more than three times longer for a fall in temperature of 10° C. Temperature thus greatly influences the decay of the facilitation process. D. M. H.

A STUDY OF THE HISTOLOGY OF THE PITUITARY GLAND OF THE SKATE

By N. H. Howes

Quart. Journ. Micr. Sci., Vol. 78, Pt. 4, 1936, pp. 637–51

A study has been made of the pituitaries of young and adult *Raia maculata* Mont., *R. clavata* L., and *R. brachyura* Laf.

The gland shows two distinct regions of growth whose size can be correlated with the size of the animal. These are situated at the anterior and posterior end of the pars anterior.

The pars anterior can be subdivided into three regions differing by the staining reactions of their constituent cells: (*a*) an anterior region where deep purple chromaphil cells are found; (*b*) a middle, where they are faintly basiphil; and (*c*) a posterior, where they are mainly acidophil.

It is suggested that these regions are homologous with the pars tuberalis, basiphil, and oxyphil areas respectively of the pars anterior of the mammalian pituitary.

The ventral lobe is a completely separate structure from the pars intermedia, although it may run along the ventral surface of the latter for some distance.

N. H. H.

ON THE PROTOZOAN PARASITES OF *CALANUS FINMARCHICUS* IN THE CLYDE SEA AREA

By Margaret W. Jepps

Quart. Journ. Micr. Sci., Vol. 79, 1937, pp. 589–658

An account is given of the parasites reputed to be of protozoan nature which where observed in *Calanus finmarchicus* in the Clyde Sea Area during the years 1933 to 1936. These comprise *Blastodinium*, *Syndinium*, some gregarines, an ectoparasitic ciliate new to science, *Paradinium*, *Ellobiopsis*, and *Ichthyo-*

sporidium, besides early stages in the development of some platyhelminth worms. A special study is made of *Paradinium*, which was plentiful throughout the summer months, and of the effect of the plasmodial parasites on their hosts.

M. W. J.

STUDIES IN SUBLITTORAL ECOLOGY. II. RECOLONIZATION AT THE UPPER MARGIN OF THE SUBLITTORAL REGION; WITH A NOTE ON THE DENUDATION OF *LAMINARIA* FOREST BY STORMS

By J. A. Kitching

Journ. Ecol., Vol. XXV, 1937, *pp.* 482–95

Recolonization of artificially denuded rock surfaces at the upper margin of the sublittoral region was followed during a period of two years. On an upward-facing horizontal surface at Dancing Ledge, Dorset, an area originally densely populated by *Corallina squamata* was colonized in the first year by *Himanthalia lorea* and various non-calcareous red algae. *Corallina* reappeared in the second year. It was concluded that normally *Corallina* excluded these early colonists by occupying all the available space. The motile fauna was little affected by changes in the algal population, but sedentary molluscs did not become established on the non-calcareous red algae.

On a denuded overhanging rock surface at a similar level in Wembury Bay, Devon, for an area originally populated by *Distomus variolosus* (Tunicate) and sponges, the sequence of recolonization was (1) *Balanus* spp. within the first half year, (2) *Lomentaria articulata* (red alga), various hydroids, *Halichondria panicea*, and *Diplosoma listerianum* (Tunicate) within the first year, (3) *Distomus variolosus* in the second year. It was concluded that *Distomus* normally restricts the earlier colonists by occupying most of the available space, but that hydroids and *Lomentaria* might remain projecting through the carpet of *Distomus*.

From an examination of *Laminaria* plants cast up by storms, it was concluded that—for the occasions in question—neither overloading of the stipes with epiphytes nor the depradations of the limpet *Patina pellucida* had contributed materially to the uprooting of the *Laminaria*. It was also concluded that in the sublittoral region *Balanus crenatus* was an early colonist of storm-denuded rock surfaces, but that this barnacle was eventually overgrown by *Laminaria*.

J. A. K.

COLOUR CHANGES IN *HIPPOLYTE VARIANS*

By L. H. Kleinholz and J. H. Welsh

Nature, Vol. 140, 1937, *p.* 851

A repetition of certain of the observations of Keeble and Gamble on colour changes of *Hippolyte varians* confirmed most of their findings. There is a distinct nocturnal blue phase and a darker day phase and these are due to changes in light conditions accompanying day and night. These phases persist, to some extent, when the eyes and eye-stalks are removed due to a direct effect of light on the chromatophores. There is in this species, however, no persisting diurnal rhythm in colour change under constant illumination or in constant darkness as claimed by Keeble and Gamble.

The crustacean eye-stalk hormone, when injected into *Hippolyte* in which the dark chromatophore pigments are dispersed, causes a concentration of these pigments and the appearance of the diffuse blue in the surrounding tissues; hence, in this respect, *Hippolyte* is like other members of the group Natantia which have been studied. J. H. W.

THE ACTIVITY OF THE HORIZONTAL SEMICIRCULAR CANAL OF THE DOGFISH, *SCYLLIUM CANICULA*

By Otto Löwenstein and A. Sand

Journ. Exp. Biol., Vol. XIII, 1936, *pp.* 416–28

The responses of the ampullary sense organ of the horizontal semicircular canal of *Scyllium* were investigated with an amplifier and oscillograph. The organ was stimulated by rotating the fish on a large turntable in the horizontal plane. It was found that these receptors, like the receptors of the lateral line, display a spontaneous activity which gives rise to a persistent discharge of impulses in the nerve. The discharge is increased during ipsilateral rotation.

During contralateral rotation the discharge is abolished or reduced. This is a type of sensory effect which has not been hitherto described. It shows how a sense organ can discriminate the two phases of a two-way stimulation. The observation helps to account for the way in which an operated animal with only one functional labyrinth can still perform reflex responses to both clockwise and anticlockwise rotation. A. S.

A COCCIDIAN FROM THE EGGS OF *THALASSEMA NEPTUNI* GAERTNER

By D. L. Mackinnon and H. N. Ray

Parasitology, Vol. XXIX, *No.* 4, 1937, *pp.* 457–67

A certain percentage of female echiurid worms of the species *Thalassema neptuni* at Plymouth have their eggs parasitized by a large sporozoan which Ray Lankester (1885) named *Monocystis thalassemae.*

The organism, although vermiform when adult, is not a gregarine. Gametogenesis and sporogony are those of a typical coccidian. The number of chromosomes is seven and the reduction division is zygotic.

The schizogonic phase occurs in the same situation as do the sexual forms, i.e. in the eggs of the host, as these lie in the genital pouches.

A new genus, *Ovivora*, is created for this sporozoan, which should now be named *Ovivora thalassemae* (Lankester). Its affinities seem to be with the Aggregatinae. D. L. M.

ON THE NERVOUS SYSTEM OF THE STARFISH *MARTHASTERIAS GLACIALIS* (L.)

By J. E. Smith

Phil. Trans. Roy. Soc., B, Vol. 227, 1937, *pp.* 111–73

This account of the distribution of the nervous elements, sensory and motor, in the starfish *Marthasterias glacialis* shows that the sensory elements are primary sense cells distributed throughout the entire ectoderm (4000 or more per sq. mm. of surface), but especially numerous in the tube feet and around the bases of the spines and pedicellariae. Below the ectoderm is a plexus of neurofibrils constituted by the central fibres of the sense cells and by the fibrillae of association ganglion cells. The subepithelial plexus is especially well developed in the radial cords, the circumoral nerve ring, and in the tube feet, where it exhibits a zoning which has been interpreted as indicating a polarity of the nervous system in that impulses are conveyed via the tube feet and radial cords to the co-ordinating centres of the circumoral nerve ring.

The motor system is represented by fibrils situated internal to the subepithelial plexus and separated from it by a boundary zone of connective tissue. The latter is, however, penetrated by neurofibrils so that the sensory and motor divisions of the system are in intercommunication.

The motor system consists of Lange's nerves—below the radial cords and nerve ring—and of a lateral motor system. The latter is made up of segmentally arranged nerves which arise at points lateral to the tube feet and opposite the adambulacral ossicles. These nerves enter the perivisceral cavity of the arms and run in the coelomic epithelium where they innervate the circular, longitudinal and apical musculature of the arms.

An account is also given of the histology of the nervous elements of the optic pits and of the sensory-motor arcs of the pedicellariae.

J. E. S.

STUDIES ON THE PHYSIOLOGY OF *ARENICOLA MARINA* L.

PART I. THE PACE-MAKER ACTION OF THE OESOPHAGUS, AND THE ACTION OF ADRENALINE AND ACETYLCHOLINE

By G. P. Wells

Journ. Exp. Biol., Vol. XIV, 1937, *p.* 117

Lugworm's were placed in glass tubes, designed to resemble the burrow, and watched. The majority showed a well-marked activity cycle, periods of anterior end activity (either proboscis extrusion or acts similar in nature but less vigorous in execution) alternating with periods of rest. Each activity cycle occupies $6{\cdot}6 \pm 2{\cdot}13$ minutes. It is suggested that *Arenicola* normally feeds in periodic outbursts, corresponding to this activity cycle.

By considering a series of dissected preparations, it can be shown that the activity cycle is due to a pace-maker action of the oesophagus. Outbursts of rhythmic activity originate in the oesophageal wall, and the excitations travel, via the neuromuscular structures in the wall of the proboscis, to the nerve ring and nerve cord, and thence to the body-wall musculature of the anterior end of the worm.

Application of adrenaline excites the oesophagus, which now discharges a continuous series of rhythmic excitations forwards into the proboscis and body wall. If intact worms are injected with adrenaline, they continue, for half an hour or longer, to show vigorous rhythmic burrowing movements. Acetylcholine causes partial contracture of the oesophagus, but does not significantly modify its normal rhythmic pattern.

Some biological implications of these results are discussed.

G. P. W.

NOTICES OF BOOKS

Marine Algae of the North-eastern Coast of North America

By William Randolph Taylor

Illustrated by Chin-Chih Jao. Ann Arbor: University of
Michigan Press, 1937. Price $5.

The book opens with a brief discussion of the geographical distribution and habitats of the algae, and useful directions as to methods of collection and preservation. There then follows a systematic list and key to the orders. Save for a casual mention in the introduction, the Myxophyceae have not been considered at all, though their description occupies over one-tenth of Prof. Newton's book on British Seaweeds. The bulk of the book consists of a description of the Chlorophyceae, Phaeophyceae and Rhodophyceae; the space they occupy is in the respective percentage proportions 19, 32 and 49. This is all excellently done, and reveals the author's intimate knowledge of his subject. In cases of doubt the type specimens have been consulted, and certain early identifications of European species have been rejected. But the author admits that certain of these have appeared and disappeared, probably several times over.

There is an ample bibliography and the sixty plates, each with numerous figures, are well chosen and well executed. The illustrations range from reductions to high magnifications.

The book is clearly printed and the price extremely reasonable. It can be warmly recommended.

W. R. G. Atkins.

An Abridged Check List and Bibliography of West North American Marine Mollusca

By A. Myra Keen. Stanford University Press

Oxford University Press: Humphrey Milford. Price 7*s*. net.

This small book includes an enormous amount of information and is extremely useful to every conchologist. Its purpose is twofold: "to systematize published information on West American Mollusca and to supply biostatigraphers with a list of midpoints-of-range corrected to date". Anyone who masters the preliminaries of the system employed, which is simple, can use this list with advantage. Those who are not statisticians will be grateful for the bibliographical information. The list is printed in imitation typewriting, but the whole volume is compact and neat.

M. V. L.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1937

Patron.

The Council has been informed that His Majesty the King has been graciously pleased to continue the Patronage granted by King Edward VIII to the Marine Biological Association of the United Kingdom.

The Council and Officers.

Four ordinary meetings of the Council have been held during the year in the rooms of the Royal Society, London, at which the average attendance was fifteen. The thanks of the Association are due to the President and Council of the Royal Society for allowing their rooms to be used.

The Council has learnt with very deep regret of the death of Mr E. T. Browne, a Governor of the Association. For many years and through times of much difficulty Mr Browne has been a staunch supporter of the Plymouth Laboratory and his death deprives the Association of one of its most generous benefactors. An obituary notice is being published in the Journal.

The Council also regrets to record the death of Mr R. L. Newman, a Governor representing the Fishmongers' Company. For a number of years Mr Newman has been a regular attendant at Council meetings and actively assisted each year in the work of the Visiting Committee appointed annually by Council to inspect the Laboratory.

The Allen Tablet.

A tablet commemorating Dr E. J. Allen's long service with the Association has been erected in the entrance hall of the Laboratory. It was unveiled by the Chairman of Council on July 8. The ceremony was attended by some members of Council, by all the Laboratory staff and visiting research workers, and by a number of Dr Allen's personal friends.

The Plymouth Laboratory.

The exterior of the Laboratory premises has been painted where needed. In the main building, at the west end, alterations and repairs effected at comparatively low cost have provided a well-equipped plunger-jar room on the first floor, improved office accommodation next door, a cloak room for laboratory attendants on the second floor, and a small store on the landing between the ground and first floors. At the same time the entrance hall and passage to the tank room, the staircase to the first floor and the passage to the main laboratory have been repainted and renovated. Plans have been approved and an order placed with G. Little and Co., Plymouth, for the replacement of certain worn-out sections of the pipe plant conveying sea water to the tank room and laboratory. Flanged glass-lined pipes and stainless steel cocks are being used throughout.

Work on the erection of a constant temperature building, situated between the north building and the Citadel wall, has been begun. The cost of the building and its equipment has been defrayed by a grant of £600 from the Rockefeller Foundation, a bequest of £150 from the estate of the late Dr Florence Buchanan and an anonymous contribution of £50.

The Aquarium.

The Aquarium has been particularly well stocked with both fish and invertebrates throughout the year and the general conditions of health have been very good. A reflector arranged above the mackerel tank has made some improvement to the lighting in what is the darkest corner of the aquarium. A shoal of over forty mackerel has recently been caught and is doing well. The number of visitors has been well up to the average of approximately 32,000 per annum, and the usual parties of school children in charge of their teachers have taken advantage of the educational value of the exhibits.

The Ship and Motor Boat.

The steam-drifter *Salpa* has given regular and satisfactory service since the completion of Lloyds' full-time survey at the end of last year. The Council is pleased to be able to report that the unforeseen expenditure incurred in the survey has been generously met by His Majesty's Treasury on the recommendation of the Development Commissioners.

The motor-boat *Gammarus* has also been in continuous commission throughout the year, although with the increasing age of the engines minor breakdowns have become more frequent.

The Staff.

Dr M. V. Lebour resumed full-time duty in April. Mr G. A. Steven was promoted to the grade of Naturalist as from April 1, 1937. In other respects the Staff remains the same as in the previous year.

Jewish Scholarship.

Dr Fabius Gross left the Laboratory at the end of September to take up an appointment as Lecturer in Experimental Zoology in the University of Edinburgh. Some of his cultures of phytoplankton organisms have been entrusted to Mr D. P. Wilson for care and maintenance. The Council have to thank the Development Commission for providing half of Dr Gross's salary for the months of August and September.

Ray Lankester Investigator.

Dr S. Ochoa, University of Madrid, was appointed Ray Lankester Investigator during the year. He commenced work at the Laboratory on July 5, for a period of five months, the subject of his research being phosphorylations in invertebrate muscle and the role of cozymase therein.

Dr Hilary B. Moore.

Dr Moore left the Laboratory at the beginning of November to take up an appointment as Assistant to the Director of the Bermuda Biological Station. He has presented to the Laboratory named collections of marine algae and barnacles and preparations showing the forms of the faecal pellets in a large number of marine animals.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year:

Dr E. Baldwin, Cambridge (Biochemistry of the electric organ of *Raia*).
Dr E. J. W. Barrington, Nottingham (Digestion in *Amphioxus*).
Dr A. M. Bidder, Cambridge (Cephalopod digestion).
Dr J. Y. Bogue, London (Library).
Dr D. Brown, New York (The respiratory rhythm and activity of the electric organ in *Raia*).
The late Mr E. T. Browne, Berkhamsted (Medusae).
J. S. Colman, Farnham (*Idotea*).
L. R. Crawshay, lately Officer for Sponge Research, British Honduras (Sponges).
P. R. Crimp, Sheffield (Microfauna).
Capt. G. C. C. Damant, Cowes (Swim bladder gases).
Dr J. F. Danielli, London (Library).
Miss M. J. Dibb, London (Life history of protozoan parasites in Polychaete worms).
E. Downing, London (Calcification of tissue).
J. E. Forrest, London (Anatomy and physiology of *Archidoris* and other Nudibranchs).
Dr Vera Fretter, London (Food storage and excretion in Molluscs. Physiology and structure of the alimentary canal in *Philine*).
Miss E. G. Geiler, Southport (*Talitrus*).
Prof. Pol Gerard, Brussels (Excretion of dyes in the Selachians).
R. Goode, Cambridge (Nerve-net in sea anemones).
Prof. E. S. Goodrich, Oxford (*Phascolosoma* and Sponges).
Mrs H. Pixell-Goodrich, Oxford (Parasites of *Phascolosoma*).
Dr F. Gross, Vienna and Berlin (Rearing of marine organisms).
Prof. A. C. Hardy, Hull (Vertical migration of plankton).
Dr F. R. Hayes, Halifax, N.S. (A quantitative study of the electrolytes in molluscan blood and muscle).
Miss P. M. Jenkin, Bristol (Diatoms).
R. R. M. Jones, Anglesey (*Littorina rudis*. Chironomid larvae. Trematode parasites of *Cardium*).
Dr B. Katz, London (Excitability of crab-nerve).
Dr J. A. Kitching, Bristol (Library).
Dr L. H. Kleinholz, Cambridge, Mass., U.S.A. (Colour change in crustaceans and fishes).
J. Ledingham, London (Nerve excitation in crabs).
Dr A. M. Lysaght, New Zealand (Breeding of *Littorina neritoides*).
Dr R. J. Lythgoe, London (Visual purple of fishes).
E. G. Macgregor, Cambridge (Nerve-net in sea anemones).
Miss M. F. Mare, Cambridge (*Upogebia*).
Dr H. Maresquelle, Strasbourg (Marine algae).
H. D. Metten, London (Ovulation in dogfish).
A. Milne, Aberdeen (Estuarine fauna).

Dr H. B. Moore, Plymouth (Littoral ecology).
Dr A. G. Nicholls, Millport (Herring biometrics).
J. A. Nicholson, Bristol (Ecology of a mud flat at Wiveliscombe).
Dr E. Steemann Nielsen, Copenhagen (Plankton).
Dr C. L. Oakley, London (Parasitic copepods from fishes).
Dr S. Ochoa, Ray Lankester Investigator (Phosphorylations in invertebrate and fish muscle).
Miss G. M. Osborne, London (Library).
Dr C. F. A. Pantin, Cambridge (Nerve-net in sea anemones).
Mrs C. F. A. Pantin, Cambridge (Feeding in sea anemones).
D. A. Parry, Bristol (Feeding and digestion in *Sagitta* and *Spadella*).
Miss D. Pelluet, Halifax, N.S. (A quantitative study of the electrolytes in molluscan blood and muscle).
E. L. Pierce, Jr., Florida (Marine plankton).
Miss M. Leyborne Popham, Bristol (Studies in the Leptonidae).
Dr R. J. Pumphrey, Cambridge (Physiology of the central nervous system of Lamellibranchs).
R. D. Purchon, Bristol (Byssus of bivalves and ciliary mechanisms in *Teredo*).
M. Ramadan, Cairo (Library. Plankton).
E. C. Reeve, Oxford (Statistical methods in allometry).
D. M. Ross, Cambridge (Nerve-net in sea anemones).
Miss A. Rothschild, London (Life cycle of Cercariae).
Miss M. Rothschild, London (Parasitic Trematodes).
A. Sandison, Cambridge (Proprioceptive reflexes in *Carcinus*).
Dr D. L. Serventy, Australia (Library).
J. E. Smith, Sheffield (Library).
J. F. Spalding, Bristol (Sexual physiology of *Carcinus*).
Miss F. A. Stanbury, Plymouth (Silica in Diatoms).
Dr E. Stauffer, Switzerland (General Zoology).
Prof. and Mrs T. A. Stephenson, Cape Town (Intertidal ecology).
Dr S. Suneson, Lund, Sweden (Life history of red algae).
Dr W. F. Thompson, Seattle, U.S.A. (General).
Miss V. Waldes, Prague (Chemical influences on barnacles).
D. A. Webb, Cambridge (Chemical relations between marine invertebrates and their environment).
G. P. Wells, London (Physiology of *Arenicola*).
Dr J. H. Welsh, Cambridge, Mass., U.S.A. (Diurnal rhythms in Crustacea).
Prof. and Mrs C. M. Yonge, Bristol (Biology of *Nucula*).
J. Z. Young, Oxford (Physiology of the nervous system of Cephalopods).
O. Zammit, Malta (General fishery work).

The usual Easter Vacation Course in Marine Biology was conducted by Mr D. P. Wilson and Mr G. A. Steven, and was attended by forty students from Oxford, Cambridge, London, Edinburgh, Dublin, Sheffield, Birmingham and Bristol.

During the Summer Vacation, a Course of Marine Biology was conducted by Prof. J. H. Orton, assisted by Miss Ruth Rawlinson. Sixteen students attended from Cambridge, London, Dublin, Liverpool, Southampton, Bristol, Aberystwyth, Plymouth and Paris.

During the Easter Vacation, Mr J. M. Branfoot brought nine students from Oundle School, Mr P. H. F. White two from Harrow, Mr A. H. Lewis three from Wellington College, Dr W. L. Francis two from Repton School, Mr C. B. Owen two from Malvern College, and Mr A. H. Pott five from Stowe School. A Botanical Class from Oxford was also held by Dr A. R. Clapham at Easter, and was attended by twelve students.

The R.R.S. *Discovery II* visited Plymouth on her homeward passage from the Antarctic on May 24, providing an opportunity for inspection by the staff of the Laboratory and visiting workers.

The Scientific Work of the Plymouth Laboratory Staff.

Physics and Chemistry of the Environment

Dr W. R. G. Atkins, in collaboration with Dr H. H. Poole, continued the photo-electric measurement of illumination and assisted in the work of the subcommittee of the International Council for the Exploration of the Sea. Provisional recommendations have been made as to the methods and aims of measurements of under-water illumination. Photo-electric cells have also been standardized for other workers.

The results published in collaboration with Prof. N. G. Ball of Colombo, using cells standardized at Plymouth, show the variation in illumination, as the sun's altitude increases up to 90°. For the spectrum as a whole the intensity is much the same at Plymouth and at Colombo, when the altitude of the sun is the same; in the violet, however, the intensity is rather less in Ceylon.

The work at sea has also been published. This was carried out with a much improved zero-resistance circuit and the usual potentiometer-amplifier-telephone null-method, using selenium rectifier cells. Extinction coefficients were obtained for infra-red, six regions in the visible spectrum, and for the ultra-violet.

Much of Dr Atkins's time has been devoted to measuring the daily light records in continuation of those already published for 1930. The first nine months of the year are now complete up to 1937, and of the eight years the sum of the daily values is closely the same for 1932, 1933, 1935, 1936 with 1937 and 1931 slightly lower and higher respectively. For 1934 appreciably higher results were obtained, and for 1930 the values are 37 % higher than for 1937.

The routine determinations of phosphate in the English Channel, started by Dr Atkins in 1923, have been continued by Dr L. H. N. Cooper. For some time it has been recognized that the ratio of nitrogen to phosphorus in the sea lies within quite narrow limits. Deviations from a standard ratio of 20 : 1 are termed "anomalies of the nitrate-phosphate ratio" and may prove of value in helping to characterize different bodies of water. Thus Mediterranean water has a high positive anomaly which can be traced for some hundreds of miles after such water has flowed into the Atlantic at a depth of about 800 metres.

A critical review of the nitrogen cycle in the sea, incorporating unpublished work, has been published in the Journal. Evidence has been produced that the oxidation of ammonia and nitrite takes place not only near the sea bottom, as is sometimes supposed, but in mid-water as well.

In collaboration with Dr Harvey, Dr Cooper has continued his studies on the iron cycle in the sea. A considerable number of measurements was made on the reactivity of various iron preparations in sea water. These were really velocity measurements and interpretation was made difficult by absence of precise knowledge of the rate at which ferrous ion reacts with dipyridyl. The work is still in progress.

Theoretical studies on the oxidation-reduction potential of sea water have been completed and published in the Journal. They made possible a further theoretical study on the solubility of different forms of iron which will appear in the Proceedings of the Royal Society. The maximum amount of ferrous ion which can exist in sea water is controlled by the amount of ferric ion and the oxidation-reduction potential of the water. The total amount of iron in true solution at equilibrium does not exceed 4×10^{-7} mg. Fe per cubic metre and of this the greater part consists of FeOH^{++} and ferrous ions.

In the course of other thermodynamical studies it was observed that the order of the anions in the lyotropic series runs closely parallel with the order of their free energies of formation, and this observation was recorded in a letter to *Nature*.

Hydrographic observations have been made throughout the year. The water of exceptionally low salinity which filled the mouth of the English Channel in 1936 has now been replaced by waters of higher and more usual salinities. The winter values of phosphate, as in recent years, are still abnormally low.

Plankton

Dr H. W. Harvey has, during the year, finished and published part of an investigation on the occurrence of iron in sea water and its utilization by diatoms. The remaining question, whether iron in stable organic combination occurs in sea water, and can be utilized, is postponed, since Dr Cooper's research on the dissociation of ferrous dipyridyl should lead to more certain methods of estimating the minute traces of iron expected.

Experiments, made during the course of this investigation on the part played by iron in the sea, have indicated that the growth rate of diatoms and the ability of their auxospores to develop are profoundly influenced by some substance or substances in the water other than phosphate, nitrate, silicate and available iron. The influence of a boiling water extract of soil on the growth of diatoms and of various larvae is known. The growth of the diatom *Thalassiosira* in artificial sea water was found (Allen, 1914) to require the addition of either natural sea water or an infusion of *Ulva*. Dr Harvey has obtained evidence that the active principle of "bios" occurring in soil and in *Ulva* is an organic acid, or mixture of acids, insoluble in alcohol and ether. The ethyl ester is soluble in ether, and when this, after it had been reconverted to the acid, was added to cultures of *Ditylum Brightwelli* and *Chlamydomonas* sp., it caused greatly increased growth. It is hoped to separate the active principle or "bios". It has properties which differ from those of α and β auxin and heteroauxin. It is stable and very resistant to bacterial decomposition and in consequence it is likely to be present in sea water.

It has also been found that cystine has a marked effect on the growth of *Ditylum*.

An experiment on the rate at which *Calanus* eat diatoms has also been made by Dr Harvey, in order to link the results of some previous experiments with observations made subsequently by other observers. The results have now been published and the investigation is being pursued further at Wood's Hole.

Mr F. S. Russell has continued the weekly examination of ring-trawl collections with reference to the occurrence of *Sagitta elegans* and *S. setosa* and associated plankton indicators of water movements. The results for 1936 have been published, and the 1937 collections have been worked through to date. The unusual conditions as regards the *Sagitta* population noticed in 1936 have continued, both species being extremely scarce until September when *S. setosa* became abundant. The autumn of 1937 was characterized by the reappearance of *Salpa fusiformis* after a period of five years.

Miss M. V. Lebour has continued her work on lamellibranch larvae and has published an account of the larva and post-larva of *Lima hians* in the Journal. A paper on prosobranch larvae has also been published in the Journal. This brings together what is known of the eggs and larvae of the British Prosobranchs with special reference to their importance in the plankton. The survey shows that our knowledge is by no means complete and many gaps have still to be filled. A very interesting new discovery is the fact that the larva of *Capulus ungaricus*, which was hatched from the egg, possesses an Echinospira larva. The Echinospira shell is much like that of *Velutina*, and it may indicate that *Capulus* is allied to the Lamellariidae and Triviinae, to which this form of larva is apparently restricted, rather than to *Calyptraea* and *Crepidula*. A paper on the larvae of *Kellia suborbicularis* is ready to be published. This mollusc is viviparous and the larvae though minute when they are set free attain a very large size in the plankton before losing the velum, thus differing widely from those of such species as the oyster which live only a few days in the free-swimming stage. Many other lamellibranch larvae have been identified by rearing them for a time. Amongst these are *Ensis* and *Cultellus*, the larvae of which can be distinguished from one another, and *Pholadidea loscombiana*, reared from artificial fertilizations until it lost the velum. The breeding seasons of many species have been ascertained, and it is noteworthy that many breed in autumn and winter.

Among the Crustacea the larvae of the two species of *Porcellana* are being specially studied as they have not as yet been distinguished. A third larva occurs in the Plymouth plankton which must belong to another species, hitherto undetected, and this is probably a *Polyonyx*. A paper on the newly hatched larva of *Spirontocaris spinus*, which differs considerably from those of related species, has been published.

Mr Russell continued his work in collaboration with the late Mr E. T. Browne on a monograph of British medusae and the preliminary typescripts of thirty-two species of Anthomedusae and three species of Leptomedusae have now been completed. Attention has again been paid to the occurrence of medusae in the weekly ring-trawl catches and a paper is now in the press reviewing the medusa population in offshore waters for the last eight years, together with notes on the biology and structure of certain species. In September the early stages of the siphonophore *Muggiaea atlantica* were reared and a short account is now ready for publication.

Mr Russell and Mr W. J. Rees have continued their research on the rearing of hydroids from medusae. They have succeeded in rearing the hydroids of *Amphinema dinema*, *Rathkea octopunctata* and *Mitrocomella brownei*, and have found the hydroid of *Amphinema rugosum*. The results of this work have been published in the Journal.

Mr Rees has in addition made a number of observations on other species. By rearing the medusae from *Clytia gracilis* he has shown that this species is in all probability only a variation of *Clytia johnstoni*. He has found a new species of *Campanulina* which, while itself indistinguishable from *C. acuminata*, produces medusae quite distinct from those of the latter species.

A close study has been made of the genus *Perigonimus*, and in this connexion Mr Rees went for a month to work at the Marine Biological Station at Herdla, near Bergen. The main object of this journey was to obtain *Perigonimus muscoides*, which is the genotype of the genus *Perigonimus*. He was fortunate in obtaining specimens of this species from which the medusae were liberated. The medusa proved to be a species of *Bougainvillia*, a discovery of considerable importance to nomenclature. A number of other interesting specimens was obtained including a hydroid which liberated a medusa which is possibly a new species of *Thamnostoma*. Many specimens of the hydroid *Heterostephanus annulicornis* were found liberating medusae which are almost certainly *Euphysa aurata*. Mr Rees had previously published in the Journal an account of a young specimen of this hydroid found at Plymouth and he has since found other specimens here.

Mr Rees received a grant from the Challenger Society to cover his expenses while working at Bergen.

Fauna of the Sea Floor (Ecology, Physiology, Genetics)

The examination of the inter-tidal estuarine fauna, particularly that of mud-flats, has made considerable progress this year. Attention has been concentrated on the Tamar Estuary, from St John's Lake to the upper reaches, and Dr H. B. Moore, Mr P. H. T. Hartley and Mr G. M. Spooner have worked in collaboration. The value of the purely biological work has been considerably enhanced by parallel investigations of various physical and chemical conditions in the estuary, conducted by other workers in the laboratory. It has become possible to envisage an ecological survey of considerable scope, and it has been agreed that various contributions shall be published in a series, with a view to bringing the results of different lines of work in as close relation to each other as possible.

Mr Spooner has paid special attention to the estimates of numbers and the general biology of the various animals encountered; he has collected material for a reference collection of estuarine bottom-living forms supplemented, where necessary, from other localities. It is hoped that a paper on the macrofauna of the inter-tidal zone will be ready before long, dealing with the density and zoning of the dominant species, such as *Nereis diversicolor*, *Nephthys hombergi*, *Scrobicularia plana*, *Cardium edule* and *Hydrobia ulvae*. While in quiet situations the mud carries an abundant fauna, it has been found that in areas subject to strong current action there is almost none at all. As is well known, the variety of species decreases rapidly up river, but the total numbers of individuals per unit area in comparable situations show no similar decline. The data are now becoming adequate for an approximate estimate of the total productivity of mudflats as a source of food for estuarine fish and wading birds, though more precise information on the rate of growth of certain species would be desirable before the calculations are put in a final form.

In connexion with this ecological survey of the estuary, Dr Cooper has collaborated with Mr A. Milne in a study of under-water illumination. They used the Pulfrich photometer with filters which divide the visible spectrum into eight approximately equal parts. Extinction coefficients in the estuary are always higher than in the English Channel. In the very turbid water red light penetrates best. They have prepared their work for publication in the Journal, where they will show the relative energy composition of under-water light and suggest ways in which this affects plant life in the estuary.

In the spring Mr D. P. Wilson studied experimentally the settling reactions of the larvae of *Notomastus latericeus*, a worm found in mud or sand. Earlier tentative results were fully confirmed. The new experiments clearly showed that larvae of this species, when provided with mud or sand, metamorphose several days before those left in clean glass vessels or with clean shell gravel. Mud perhaps induces slightly more rapid settling than does sand. A paper has been published which records these results and discusses their bearing on problems concerning the distribution of the bottom fauna.

A description of an unusual specimen of *Eulalia* with a secondary tail has been published. In the majority of known examples of bifurcation in annelids the forking has been lateral, whereas in this specimen it was dorso-ventral, originating probably through injury to the ventral nerve cord.

During the past three years Mr Wilson has been keeping a regular record of tank temperatures and the habits and death rate in the aquarium of *Sepia officinalis*. Deaths tend to occur during or shortly after falls in temperature such as are brought about by frosty weather. Owing, however, to the present impossibility of controlling the temperature of a large tank results are sometimes difficult to interpret. It is nevertheless clear that below about 11° C.

little or no feeding takes place and the *Sepia* are relatively sluggish and in poor health.

Continuing his experiments on the physiology of the sense organs of fishes Dr A. Sand has completed the first part of an investigation on the lateral line, and this has been published in the Proceedings of the Royal Society. The main results of this work were obtained by a special technique for recording the discharge of impulses in single fibres of the lateral-line nerves when a portion of a lateral-line canal of the ray was perfused with elasmobranch ringer at a controlled rate of flow. This procedure has revealed the great sensitivity of the sense organs to movement of fluid in the canal, and has established the exact proportionality between the rate of flow and the frequency of impulse discharge. The behaviour of this sensory system with reference to displacement of the fluid in the lateral-line canals turns out to be fundamentally the same as that of the sense organs of the semicircular canals of the labyrinth with respect to angular accelerations, as studied last year by Löwenstein and Sand. But whereas in the semicircular canals the sensory mechanism serves to record angular displacement in space, in the lateral-line canals it serves for the perception of vibrations coming from a distance, and the way in which the impulse discharges follow the frequency of low tones, audible to the human ear, produced in the neighbourhood of the fish, justifies the description of the lateral-line system as a form of auditory organ.

Closely associated with the lateral-line organs in elasmobranch fishes are the ampullary canals of Lorenzini. Practically nothing is known concerning their function and Dr Sand has recently begun to study them. So far it has been established that, like the organs of the lateral line and of the labyrinth, they exhibit the property of spontaneous rhythmical nervous activity, and that their specific sensory function is entirely different from that of the other two sensory systems. This work is being continued.

In the course of the year the joint paper by Fessard and Sand on the muscle proprioceptors of the ray has been published in the Journal of Experimental Biology.

Mrs E. W. Sexton and Miss A. R. Clark have continued the experimental work on *Gammarus chevreuxi*, designed to determine the frequency of heterozygosis in the wild.

A sample of 5000 black-eyed animals was taken from a new locality at the head of the tidal water of the River Tavy. Owing probably to the continuous high temperatures during the summer there has been a great mortality in the bowls in the laboratory, and the numbers obtained are not sufficient for satisfactory conclusions. It has, however, been demonstrated that heterozygotes can be obtained from this population, similar to those previously found in Chelson Meadow, and the work is still being carried on.

Considerable progress has been made during the year in putting the charts and records of the whole work on a permanent basis, so that they can be made available for reference and further study at any time in the future.

Fish and Fisheries

Mr E. Ford has completed his first paper on Vertebral Variation in Teleostean Fishes. Thanks to a grant from the Royal Society it has been possible to publish this in the Journal, together with 16 Plates reproducing photographs. The work takes the form of a broad survey of the many interesting and important problems arising from the study of the teleostean backbone, exemplified by extensive data on upwards of one hundred species. Material has been collected for a detailed report on vertebral variation in clupeoid fishes, including the herring.

Mr Ford carried out a routine survey of the winter herring drift-net fishery at Plymouth during the season 1936–37 as in former years. As was to be feared from a knowledge of the condition of the fishery stock during recent years, the yield was again very disappointing. Only 56 East Country steam drifters and 26 Cornish motor drifters participated, and the combined catch for the two fleets during the two months of December 1936 and January 1937 was no more than 3040 cwt. How serious the position has become is shown by a comparison with corresponding figures for the season 1930–31 when 75 Lowestoft steamers and 177 Cornish motors landed a total of 94,811 cwt. valued at £52,973. Indeed, in a number of seasons in the past, landings on a single day have frequently exceeded the total catch for the season 1936–37. As stated in the Report of Council for 1935 and 1936, the paucity of fish on the grounds seems to be the result of the absence of young fish in the visiting shoals since about 1931–32. Why this should be, and when a change for the better may be expected, are questions of the greatest concern. Unfortunately it is not yet possible to answer them.

The lectures on the Nation's Sea-Fish Supply which were delivered by Mr Ford as Buckland Professor for 1936, were published in book form in June.

Mr G. A. Steven, assisted by Mr P. G. Corbin, has continued throughout the year his researches into the biology of the mackerel in western waters. With a view to ascertaining ages and growth rates otoliths have now been collected from 3561 fish. As mentioned in last year's report it is impossible to collect scales from ordinary samples of fish landed on the fishmarkets owing to the extreme smallness of the scales, which are very easily dislodged when one fish rubs against another. As, however, it has been highly desirable to supplement otolith readings with scale readings in as many fish as possible, suitable envelopes have been made into which fish for examination are placed immediately on capture; these have been supplied to selected fishermen. This method has been found to work well with line-caught fish which can be placed straight into the envelopes without handling. It is less successful with drift-net samples as each fish has to be grasped in the hand in order to remove it from the net. In this way most of the scales are rubbed off and other scales which do not belong to the fish become attached to it. Trawl and seine caught fish are always completely devoid of scales.

This year's work has confirmed last year's preliminary finding that the otoliths are readable in the younger fish—i.e. in those having up to three or four broad (? summer) zones in the otoliths. Where unadulterated scale samples have been obtained they agree with the otolith readings. The data thus acquired, though still insufficient for the precise determination of ages and growth rates, are already producing encouraging results.

Examination of the gonads of some 1600 female fish has shown that the mackerel does not get rid of all of one season's eggs in one brief spawning period, as does the herring. The eggs ripen in successive batches. Thus the spawning period of each individual fish and therefore of the population as a whole, is a lengthy one, extending, it appears, over several months of the spring and early summer. This successive ripening of the eggs in the mackerel ovary renders the already established scales of maturity stages inapplicable to this fish. Efforts are being made to devise some other method which can successfully be applied.

One of the major difficulties encountered in elucidating the life-history of the mackerel is the difficulty in obtaining young post-larval fish from 2 to 15 cm. in length. In all the history of fishery investigations only a very few isolated individuals between these sizes have been caught. It is therefore encouraging to report that large numbers of young stages from 9 cm. in length upwards have been obtained during the present year.

Some three thousand skeletons have been prepared and examined with a view to ascertaining whether distinctive racial characters exist. The total number of vertebrae is remarkably constant at 31. It has been found, however, that the number of thoracic vertebrae without haemal arches is variable—9 or 10; rarely 8 or 11—but further data are required before it can be established whether or not this variant has any significance.

Three cruises have been made this year in search of mackerel eggs and larvae, and for the collection of general plankton samples from the mackerel fishing and spawning grounds. One cruise took place in April in the Ministry's research ship *George Bligh*, one in May in a steam drifter, and one in July in a steam trawler. These cruises covered a considerably larger area than could be sampled last year. Examination of the material collected is not yet complete, but will show something of the distribution in space and time of the spawning activities of the mackerel and of the dispersal of the larvae. Last year larval mackerel were collected west of the Channel mouth as early as April 29, which pointed to the probability of spawning activities at least as early as mid-April. This probability was confirmed in April of this year when the westerly plankton samples were found to contain large numbers of mackerel eggs.

The material so far collected has been examined for a possible Sagitta-mackerel correlation.

Plankton samples have also been collected on the fishing grounds by selected commercial drifters working from Newlyn, but these samples have yet to be examined.

The International Council for the Exploration of the Sea, acting on the recommendation of their Atlantic Slope Committee, has appointed a subcommittee for the study of technical methods in mackerel researches. This subcommittee, which comprised representatives of Denmark, France, Germany, Portugal, the Irish Free State and England, met at the Plymouth Laboratory on December 8 and 9.

The observations on the seasonal abundance of the pelagic stages of young fishes have been continued by Mr F. S. Russell throughout the year 1937. The results for the year 1936 have been published in the Journal. In 1937 there has been a repetition of the conditions shown in 1936. The normal peak of the young of spring spawners has been almost completely absent, while there has been a slight improvement in the numbers of young of summer spawners. The year, like 1936, has been remarkable for the numbers of pilchard eggs in the plankton which have continued without interruption from April to November.

Mr P. H. T. Hartley has continued his investigation of the tuck-net fishery in the river Tamar. Monthly examinations have been made of the food of all species of fish taken in the net.

The flounder has been the subject of a special study. In addition to the length and stomach contents of each fish, the weight, sex, gonad condition and otolith reading were recorded. The fish were then handed to Mr D. P. Wilson for examination of the fat content. Mature flounders leave the river at the end of January and go down to the sea to spawn on muddy grounds a few miles offshore. Some females return to brackish water after spawning; but no spent males have been taken in the estuary. Few flounders are taken in the tuck-net during the summer months. The local fishermen say that they wander away among the saltings of the tidal creeks. Attempts were made to catch them there, with fish-spears at low tide, but with little success.

In order to obtain some exact data on growth rates and to investigate the movements of flounders within the estuary, a marking scheme was begun in September, 1937. By November 15, 813 fish had been marked and released at six stations. Several recoveries have already been made, the most remarkable being an 18 cm. female caught in a surface drift-net in 40 feet of water.

For plaice and dabs the estuary is largely a nursery ground. In 1937 the number of O-group fishes of these two species which came into the river mouth was much smaller than in the previous year. O-group flounders are rarely taken in the tuck-net.

Mr Hartley gave some assistance in the Mackerel Investigations in connexion with the vertebral counts and has cooperated with Mr Spooner and Dr Moore in an enquiry into the distribution and ecology of the fauna of the Tamar estuary. During the winter 1937–38 it is hoped to investigate the food of the wading birds by the examination of crop contents.

In his investigations into the histologically stainable fat in the muscular body regions of fishes Mr D. P. Wilson has been paying particular attention to the flounder. This species was chosen for detailed study because of the possibility of utilizing Mr Hartley's material from the River Tamar after the stomach contents etc. had been recorded. Information would thus be available which might in due course be correlated with the fat content. This expectation has to some extent been realized.

In the flounder, as in probably most fishes, there is undoubtedly considerable variation in fatness between individuals irrespective of size, sex or season; it seems evident that some naturally tend to fatness and others to leanness. However, the examination of four to five hundred flounders throughout the year has shown that in general they are lean about February, after a period of slack feeding during the winter, and are fattest in September and October after good summer feeding. A fact of interest is the discovery in some specimens of minute drops of intracellular fat in the fibres of the superficial lateral muscle. It is possible that their presence may eventually be correlated with a stage in the reproductive cycle. At the moment the matter is still being investigated, but results so far point to the deposition of this fat in maturing fish prior to spawning and its loss at or shortly after that event.

Dr Atkins was called upon to advise upon a number of questions in connexion with the preservation of nets and ropes. The clearance of the outlet of the Cawsand fish-pond rendered this again available for immersion tests. Herring-nets treated by about three dozen methods showed that a mixture of copper oleate and coal tar and a new modification of the old cutch bichromate treatment were the best. The tests are being continued to ascertain which of the two is the better. Similar tests with trawl twines are in progress and the herring-net results suggested further modifications which have still to be tested. Two rafts have been constructed and moored in the Sound for anti-fouling tests which are being carried out on behalf of the Admiralty and a firm of paint manufacturers.

The Library.

The thanks of the Association are again due to numerous Foreign Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the Journal. Thanks are also due to those authors who have sent copies of their books or papers, which are much appreciated.

In accordance with a decision of the Council the printing and publication of the Journal has been transferred to the Cambridge University Press. The change took effect from Vol. XXII, No. 1, which was issued in November. The width of the page has been increased in order to give more space for plates and tables, the height remaining unaltered. The revised lay-out of the cover includes a new drawing of the Laboratory.

Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association.

Atkins, D., 1936. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part I. New observations on sorting mechanisms. *Quart. Journ. Micr. Sci.*, Vol. lxxix, pp. 181–308.

Atkins, D., 1937. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part II. Sorting devices on the gills. *Quart. Journ. Micr. Sci.*, Vol. lxxix, pp. 339–373.

Atkins, D., 1937. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part III. Types of Lamellibranch gills and their food currents. *Quart. Journ. Micr. Sci.*, Vol. lxxix, pp. 376–421.

Atkins, D., 1937. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part IV. Cuticular fusion, with special reference to the fourth aperture in certain Lamellibranchs. *Quart. Journ. Micr. Sci.*, Vol. lxxix, pp. 423–445.

Atkins, W. R. G., 1937. The transmission of light and total radiation by leaves. *Proc. Roy. Soc. Lond.*, Ser. B., Vol. cxxii, pp. 26–29.

Atkins, W. R. G., 1937. Note on the use of sodium diethyldithiocarbamate for detecting the solubility corrosion of metals. *Trans. Faraday Soc.*, Vol. xxxiii, pp. 431–432.

Atkins, W. R. G., Ball, N. G. and Poole, H. H., 1937. The photo-electric measurement of the diurnal variations in daylight in temperate and tropical regions. *Proc. Roy. Soc. Lond.*, Ser. A, Vol. clx, pp. 526–539.

Bacq, Z. M., 1937. Nouvelles observations sur l'acétylcholine et la choline-estérase chez les invertébrés. *Arch. Int. Physiol.*, T. xliv, pp. 174–189.

Bacq, Z. M., 1937. L'"Amphiporine" et la "némertine" poisons des vers némertiens. *Arch. Int. Physiol.*, T. xliv, pp. 190–204.

Bacq, Z. M. and Nachmansohn, D., 1937. Cholinesterase in invertebrate muscles. *Journ. Physiol.*, Vol. lxxxix, pp. 368–371.

Berrill, N. J. and Cohen, A., 1936. Regeneration in *Clavelina lepadiformis*. *Journ. Exp. Biol.*, Vol. xiii, pp. 352–362.

Cooper, L. H. N., 1937. A relation between the lyotropic series and free energies. *Nature*, Vol. cxxxix, pp. 284–285.

Dennell, R., 1937. On the feeding mechanism of *Apseudes talpa*, and the evolution of the Peracaridan feeding mechanisms. *Trans. Roy. Soc. Edin.*, Vol. lix, pp. 57–78.

Fessard, A. and Sand, A., 1937. Stretch receptors in the muscles of fishes. *Journ. Exp. Biol.*, Vol. xiv, pp. 383–496.

Fischer, E., 1936. The action of a single vagal volley on the heart of the eel and the turtle. *Amer. Journ. Physiol.*, Vol. cxvii, pp. 596–608.

Ford, E. *The Nation's Sea-Fish Supply*. Buckland Lectures for 1936. (London, 1937.)

Fretter, V. 1937. The structure and function of the alimentary canal of some species of *Polyplacophora* (Mollusca). *Trans. Roy. Soc. Edin.*, Vol. lix, pp. 119–164.

Frost, Nancy, 1936. I. Amphipoda from Newfoundland waters. II. Decapod larvae from Newfoundland waters. *Newfoundland Dept. of Natural Resources, Division of Fish Research. Reports. Faunistic Series*, No. 1.

Gross, F., 1937. The life-history of some marine plankton diatoms. *Phil. Trans. Roy. Soc.*, Ser. B, Vol. ccxxviii, pp. 1–48.

Hall, D. M. and Pantin, C. F. A., 1937. The nerve net of the Actinozoa. V. Temperature and facilitation in *Metridium senile*. *Journ. Exp. Biol.*, Vol. xiv, pp. 71–78.

Hörstadius, S., 1936. Studien über heterosperme Seeigelmerogone nebst Bemerkungen übereinige Keimblattchimären. *Mém. Acad. Roy. d'Hist. Nat. Belg.*, Sér. 2, fasc. 3, pp. 801–880. Mélanges Paul Pelseneer.

Jepps, M. W., 1937. On the protozoan parasites of *Calanus finmarchicus* in the Clyde sea area. *Quart. Journ. Micr. Sci.*, Vol. LXXIX, pp. 589–658.

Kitching, J. A., 1937. Studies in sublittoral ecology. II. Recolonisation at the upper margin of the sublittoral region; with a Note on the denudation of *Laminaria* forest by storms. *Journ. Ecology*, Vol. XXV, pp. 482–495.

Kleinholz, L. H. and Welsh, J. H., 1937. Colour changes in *Hippolyte varians*. *Nature*, Vol. CXL, pp. 851–852.

Mackinnon, Doris L. and Ray, H. N., 1937. A coccidian from the eggs of *Thalassema neptuni* Gaertner. *Parasitology*, Vol. XXIX, pp. 457–468.

Nolte, W., 1936. Annelidenlarven. *Nordisches Plankton*, Lief. XXIII, pp. x, 59–169.

Nolte, W., 1937. Die Zucht und Konservierung der Polychaetenlarven. *Journ. du Conseil*, Vol. XII, pp. 51–76.

Poole, H. H. and Atkins, W. R. G., 1937. The penetration into the sea of light of various wave-lengths as measured by emission or rectifier photo-electric cells. *Proc. Roy. Soc.*, Ser. B, Vol. CXXIII, pp. 150–165.

Russell, F. S., 1937. Drift through the English Channel as shown by plankton distribution. *Assoc. Oceanogr. Phys.*, *Proc. Verb.*, No. 2, pp. 137–138.

Sand, A., 1937. Peripheral excitation and inhibition of a sense organ. *Journ. Physiol.*, Vol. LXXXIX, pp. 47 *P*–49 *P*.

Sand, A., 1937. The mechanism of the lateral sense organs of fishes. *Proc. Roy. Soc. Lond.*, Ser. B, Vol. CXXIII, pp. 472–495.

Smith, J. E., 1937. On the nervous system of the starfish *Marthasterias glacialis* (L.). *Phil. Trans. Roy. Soc. Lond.*, Ser. B, Vol. CCXXVII, pp. 111–173.

Vanderbroek, G., 1937. Les mouvements protoplasmiques au cours de la fécondation de l'oeuf Ascidie. *Arch. f. exp. Zellforsch.*, Bd. XIX, pp. 411–419.

Wells, G. P., 1937. Studies on the physiology of *Arenicola marina* L. I. The pacemaker role of the oesophagus, and the action of adrenaline and acetylcholine. *Journ. Exp. Biol.*, Vol. XIV, pp. 117–157.

Wilson, D. P., 1936. The Plunger Jar. *The Aquarist and Pond-keeper*, Vol. VII, pp. 138–139.

Wilson, D. P., 1937. Photography and the work of the Marine Biological Laboratory. *The Photographic Journ.*, April, pp. 176–184.

Wilson, D. P., 1937. Fishes of a rocky sea-shore. *The Aquarist and Pond-keeper*, Vol. VII, pp. 240–242.

Winton, F. R., 1937. The changes in viscosity of an unstriated muscle (*Mytilus edulis*) during and after stimulation with alternating, interrupted and uninterrupted direct currents. *Journ. Physiol.*, Vol. LXXXVIII, pp. 492–511.

Wykes, Ursula. The photic control of pigmentary responses in teleost fishes. *Journ. Exp. Biol.*, Vol. XIV, pp. 79–86.

Membership of the Association.

Governors. Two of the Governors appointed by the Fishmongers' Company have changed during the year. The new Prime Warden is Col. The Hon. Angus McDonnell, C.B., and the place of the late Mr R. L. Newman has been taken by Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O.

Founders. As last year, the number of Founders has been 44, of whom 18 are living.

Vice-Presidents. The Council regret to record the death of two Vice-Presidents, Sir Austen Chamberlain and Dr G. A. Boulenger. Mr Walter E. Elliott on leaving the Ministry of Agriculture and Fisheries has resigned from the Association, and Mr W. S. Morrison, who has succeeded him as Minister, has been proposed in his place as a Vice-President.

Annual Members. The total number of annual members on Jan. 1 1938 was 284, of whom 15 were elected during the year. This is a net increase of 6 over the total of 278 annual members on Jan. 1 1937.

Associate Members. The number of Associate Members has been increased to 4 by the election of Miss Maude Delap.

Finance.

The Council have this year to express their thanks to the Development Commissioners, not only for their continued support of the general work of the Laboratory, but for special assistance to meet unforeseen contingencies, such as the heavy additional cost of the repairs to the *Salpa.* They are also grateful for generous grants from the Fishmongers' Company (£600), the Royal Society (£100 + £55 towards cost of publication of Mr Ford's paper in Vol. XXII, No. 1, of the Journal), the British Association (£50), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52. 10*s.*), London (£52. 10*s.*), Bristol (£25), Birmingham (£15. 15*s.*), Manchester (£10. 10*s.*), Leeds (£10. 10*s.*), Sheffield (£5. 5*s.*), the Imperial College of Science and Technology (£10), and the Cornwall Sea Fisheries Committee (£10).

The Council are also deeply appreciative of the generous benefactions of £600 from the Rockefeller Foundation, £150 from the estate of the late Miss Florence Buchanan and an anonymous donation of £50, which have made possible the provision of a constant temperature plant at the Laboratory.

Vice-Presidents, Officers and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1938–39.

President

The Lord Moyne, P.C., D.S.O.

Vice-Presidents

The Duke of Bedford, K.G.
The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
The Earl of Iveagh, C.B., C.M.G.
Viscount Astor
Lord St Levan, C.B., C.V.O.
The Right Hon. W. S. Morrison, M.C., K.C., M.P.
Lord Noel-Buxton, P.C.
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S.
Sir Nicholas Waterhouse, K.B.E.
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S.
J. O. Borley, Esq., O.B.E.
Col. E. T. Peel, D.S.O., M.C.

COUNCIL

To retire in 1939

Sir Joseph Barcroft, C.B.E., F.R.S.
M. Burton, Esq., D.Sc.
E. S. Russell, Esq., O.B.E., D.Sc.
J. M. Tabor, Esq.

To retire in 1940

Prof. H. Graham Cannon, Sc.D., F.R.S.
Capt. G. C. C. Damant, R.N., C.B.E.
H. Muir Evans, Esq., M.D.
Prof. F. E. Fritsch, D.Sc., F.R.S.
C. F. A. Pantin, Esq., Sc.D., F.R.S.
J. Z. Young, Esq.

To retire in 1941

R. S. Clark, Esq., D.Sc.
A. C. Gardiner, Esq.
Prof. A. C. Hardy, D.Sc.
Prof. A. V. Hill, O.B.E., Sc.D., F.R.S.
Prof. D. L. Mackinnon, D.Sc.

Chairman of Council

Prof. E. W. MacBride, D.Sc., F.R.S.

Hon. Treasurer

Guy Wood, Esq., M.B., M.R.C.P., 99 Sydenham Hill, London, S.E. 26

Secretary

Stanley Kemp, Esq., Sc.D., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. Bidder, Esq., Sc.D.
The Lord Moyne, P.C., D.S.O.
H. G. Maurice, Esq., C.B. (Ministry of Agriculture and Fisheries)
Col. The Hon. Angus McDonnell, C.B. (Prime Warden of the Fishmongers' Company)
Guy Wood, Esq., M.B., M.R.C.P. (Fishmongers' Company)
Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O. (Fishmongers' Company)
Prof. E. S. Goodrich, D.Sc., F.R.S. (Oxford University)
Prof. J. Gray, M.C., Sc.D., F.R.S. (Cambridge University)
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S. (British Association)
Prof. E. W. MacBride, D.Sc., F.R.S. (Zoological Society)
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S. (Royal Society)
E. J. Allen, Esq., C.B.E., D.Sc., F.R.S. (*Honorary*)

LIST OF ANNUAL SUBSCRIPTIONS

Paid during the year, April 1 1937 to March 31 1938

	£	s.	d.
E. J. Allen, Esq., C.B.E., D.SC., F.R.S.	1	1	0
Dr I. Amemiya	1	1	0
Miss D. Atkins	1	1	0
E. Baldwin, Esq.	1	1	0
Prof. Sir Joseph Barcroft, F.R.S.	1	1	0
Miss M. G. Barnes	1	1	0
W. H. Barrett, Esq.	1	1	0
Dr J. B. Bateman	1	1	0
L. C. Beadle, Esq.	1	1	0
R. L. A. Beauchamp, Esq.	1	1	0
G. R. de Beer, Esq.	1	1	0
Miss C. R. Begg	1	1	0
J. Bělehrádek, Esq., M.D.	1	1	0
N. J. Berrill, Esq., D.SC. (1932, 1933, 1934, 1935, 1936)	5	4	0
D. M. Bickmore, Esq.	1	1	0
Birkbeck College	1	1	0
W. Birtwistle, Esq.	1	1	0
Dr H. Blaschko (1937 and 1938)	2	2	0
H. H. Bloomer, Esq.	1	1	0
H. Moss Blundell, Esq., C.B.E.	1	1	0
Dr B. G. Bogorov	1	1	0
Dr J. Yule Bogue	1	1	0
Capt. R. J. B. Bolitho	1	1	0
J. O. Borley, Esq., O.B.E. (1929, 1930, 1931, 1932, 1933, 1934, 1935, 1936, 1937)	9	9	0
Dr J. Borowik	1	1	0
L. A. Borradaile, Esq., SC.D.	1	1	0
Prof. C. L. Boulenger	1	1	0
Col. Sir Henry Bowles, Bart.	1	1	0
A. Bowman, Esq., D.SC.	1	1	0
The late Prof. A. E. Boycott, F.R.S.	1	1	0
J. M. Branfoot, Esq. (1936 and 1937)	2	2	0
Brighton Public Library	1	1	0
L. R. Brightwell, Esq.	1	1	0
Bristol Grammar School	1	1	0
Bristol University	1	1	0
Miss E. M. Brown	1	1	0
H. H. Brown, Esq.	1	1	0
Dr H. O. Bull	1	1	0
W. S. Bullough, Esq.	1	1	0
R. H. Burne, Esq., F.R.S.	1	1	0
M. Burton, Esq., D.SC.	1	1	0
L. W. Byrne, Esq.	1	1	0
Prof. H. Graham Cannon, SC.D., F.R.S.	1	1	0
J. N. Carruthers, Esq., D.SC.	1	1	0
Dr G. S. Carter	1	1	0
Charterhouse School	1	1	0
P. T. Clothier, Esq.	1	1	0
Coastguard and Fisheries Service, Alexandria	1	1	0
Prof. F. J. Cole, D.SC., F.R.S.	1	1	0
H. A. Cole, Esq.	1	1	0
J. S. Colman, Esq.	1	1	0
P. G. Corbin, Esq. (1938 and 1939)	2	2	0
C. A. Cosway, Esq.	1	1	0
Col. R. Stapleton Cotton	1	1	0
G. I. Crawford, Esq.	1	1	0
L. R. Crawshay, Esq.	1	1	0
P. R. Crimp, Esq.	1	1	0
Miss D. R. Crofts	1	1	0
Sir H. H. Dale, C.B.E., M.D., F.R.S.	1	1	0
Dr H. H. Darby (1935, 1936, 1937, 1938 and 1939)	5	5	0
Dr W. Cameron Davidson (1935, 1936 and 1937)	3	3	0
S. B. Davie, Esq.	1	1	0
F. M. Davis, Esq.	1	1	0
Ben Dawes, Esq., D.SC.	1	1	0
Department of Fisheries, Bangkok	1	1	0
Division of Fisheries, Capetown	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
F. M. Dyke, Esq.	1	1	0
Prof. L. E. S. Eastham	1	1	0
P. Eggleton, Esq., D.SC.	1	1	0
Dr Hussein Faouzi (1936 and 1937)	2	2	0
G. P. Farran, Esq. (1937 and 1938)	2	2	0
Miss R. Fellowes	1	1	0
Prof. R. A. Fisher, SC.D., F.R.S.	1	1	0
Miss K. M. G. Flemming (1937 and 1938)	2	2	0
E. Ford, Esq.	1	1	0
E. B. Ford, Esq.	1	1	0
Dr G. H. Fowler	1	1	0
C. L. Fox, Esq.	1	1	0
Prof. H. Munro Fox, F.R.S.	1	1	0
Miss E. A. Fraser, D.SC.	1	1	0
Prof. F. E. Fritsch, D.SC., F.R.S.	1	1	0
A. C. Gardiner, Esq.	1	1	0
Prof. J. Stanley Gardiner, F.R.S.	1	1	0
Adrian Gardner, Esq.	1	1	0
Major Austin Gardner, M.C.	1	1	0
S. G. Gibbons, Esq. (1933, 1934, 1935 and 1936)	4	4	0
H. C. Gilson, Esq.	1	1	0
Prof. E. S. Goodrich, D.SC., F.R.S.	1	1	0
Alastair Graham, Esq.	1	1	0
Michael Graham, Esq.	1	1	0
Ronald Grant, Esq.	1	1	0
Dr A. H. M. Gray	1	1	0
Prof. J. Gray, M.C., SC.D., F.R.S.	1	1	0
Prof. A. C. Hardy, D.SC.	1	1	0

	£	s.	d.
Prof. C. R. Harington, F.R.S.	1	1	0
Dr J. E. Harris (1936 and 1937)	2	2	0
P. H. T. Hartley, Esq.	1	1	0
Prof. L. A. Harvey	1	1	0
G. T. D. Henderson, Esq., D.SC.	1	1	0
C. C. Hentschel, Esq.	1	1	0
C. F. Hickling, Esq. (1937 and 1938)	2	2	0
Prof. Sydney J. Hickson, D.SC., F.R.S.	1	1	0
Prof. A. V. Hill, F.R.S.	1	1	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
M. A. C. Hinton, Esq.	1	1	0
Prof. K. Hirasaka	1	1	0
Prof. A. D. Hobson (1935, 1936, 1937)	3	3	0
Prof. L. T. Hogben, D.SC.	1	1	0
Dr E. G. Holmes	1	0	0
F. R. Horne, Esq.	1	1	0
H. D. Howell, Esq.	1	1	0
N. H. Howes, Esq.	1	1	0
Hull University College	1	1	0
O. D. Hunt, Esq.	1	1	0
Prof. J. S. Huxley	1	1	0
Miss P. M. Jenkin	1	1	0
Miss M. Jepps	1	1	0
Jersiaise, Conservateur Honoraire du Musée de la Société	1	1	0
D. D. John, Esq.	1	1	0
Rodney R. M. Jones, Esq.	1	1	0
J. J. Judge, Esq.	1	1	0
Stanley Kemp, Esq., SC.D., F.R.S.	1	1	0
Mrs A. Redmond King	1	1	0
P. Kirtisinghe, Esq.	1	1	0
Dr J. A. Kitching	1	1	0
Dr J. Kollmann	1	1	0
Dr G. Lapage	1	1	0
Prof. R. D. Laurie	1	1	0
Major R. H. Leigh, R.A.M.C.	1	1	0
D. W. le Mare, Esq.	1	1	0
A. G. Lowndes, Esq.	1	1	0
C. E. Lucas, Esq.	1	1	0
Adrian Lumley, Esq.	1	1	0
Miss Averil Lysaght	1	1	0
Prof. E. W. MacBride, D.SC., F.R.S.	1	1	0
R. MacDonald, Esq.	1	1	0
Lt.-Col. W. Mackenzie, O.B.E.	1	1	0
Prof. D. L. Mackinnon, D.SC.	1	1	0
N. A. Mackintosh (1937 and 1938)	2	2	0
G. I. Mann, Esq.	1	1	0
Sir John D. Marsden, Bart., J.P.	1	1	0
H. G. Maurice, Esq., C.B.	1	1	0
Dr Cyril F. Mayne, O.B.E., F.R.C.S. (1937, 1938 and 1939)	3	3	0
Capt. W. N. McClean	1	1	0
C. R. McKenzie, Esq.	1	1	0
Milford Haven Trawler Owners Association, Ltd.	1	1	0
W. S. Millard, Esq.	1	1	0
Norman Millott, Esq.	1	1	0
Sir Peter Chalmers Mitchell, Kt., C.B.E., F.R.S.	1	1	0
Mrs E. M. Morehouse	1	1	0

	£	s.	d.
C. C. Morley, Esq.	1	1	0
The Rt. Hon. W. S. Morrison, M.C., M.P.	1	1	0
Mount Pleasant Island Biological Laboratory	1	1	0
L. L. Mowbray, Esq.	1	0	0
Dr J. Mukerji	1	1	0
National Museum of Wales	1	1	0
Morley H. Neale, Esq.	1	1	0
Messrs Neale and West, Ltd.	1	1	0
Dr A. G. Nicholls	1	1	0
J. A. Nicholson, Esq.	1	1	0
J. R. Norman, Esq.	1	1	0
Dr C. L. Oakley	1	1	0
Office Scientifique et Technique des Pêches Maritimes, La Rochelle (1937 and 1938)	2	2	0
Office Scientifique et Technique des Pêches Maritimes, Port de l'Orient Keroman (1937 and 1938)	2	2	0
Prof. Y. Okada (1935, 1936 and 1937)	3	3	0
Charles Oldham, Esq.	1	1	0
G. W. Olive, Esq.	1	1	0
J. Omer-Cooper, Esq. (1937 and 1938)	2	2	0
Prof. J. H. Orton, D.SC.	1	1	0
Miss G. M. Osborne	1	1	0
The Hon. John H. Parker (1937 and 1938)	2	2	0
D. A. Parry, Esq. (1937 and 1938)	2	2	0
C. W. Parsons, Esq.	1	1	0
W. N. Paton, Esq.	1	1	0
Messrs Pawlyn Bros.	1	1	0
T. A. Pawlyn, Esq.	1	1	0
Messrs Peacock and Buchan, Ltd.	1	1	0
Pease Laboratories Incorporated	1	1	0
Colonel E. T. Peel, D.S.O., M.C.	1	1	0
F. T. K. Pentelow, Esq.	1	1	0
Prof. E. Percival (1937 and 1938)	2	2	0
L. E. R. Picken, Esq.	1	1	0
Plymouth Corporation (Museum Committee)	1	1	0
Plymouth Educational Authority	1	1	0
Plymouth Proprietary Library	1	1	0
Plymouth Public Library	1	1	0
Miss M. L. Popham (1938 and 1939)	2	2	0
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
Portsmouth Municipal College	1	1	0
Queen Mary College	1	1	0
Dr H. E. Quick, F.R.C.S.	1	1	0
W. J. Rees, Esq.	1	1	0
H. C. Regnart, Esq.	1	1	0
D. M. Reid, Esq.	1	1	0
Prof. L. P. W. Renouf	1	1	0
E. A. Robins, Esq. (1937 and 1938)	2	2	0
Lord Rothschild	1	1	0
C. H. Rudge, Esq. (1938 and 1939)	2	2	0

	£	s.	d.
E. S. Russell, Esq., D.SC.	1	1	0
F. S. Russell, Esq., D.S.C., D.F.C., F.R.S.	1	1	0
Capt. the Hon. Lionel St Aubyn, M.V.O.	1	1	0
The Rt. Hon. Lord St Levan, C.B., C.V.O.	1	1	0
Dr A. Sand	1	1	0
J. T. Saunders, Esq.	1	1	0
R. E. Savage, Esq.	1	1	0
W. L. Sclater, Esq.	1	1	0
B. Sen, Esq.	1	1	0
Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S.	1	1	0
Miss Lilian Sheldon	1	1	0
Prof. W. Rae Sherriffs, D.SC.	1	1	0
H. P. Sherwood, Esq.	1	1	0
B. Webster Smith, Esq.	1	1	0
F. G. W. Smith, Esq.	1	1	0
J. E. Smith, Esq.	1	1	0
Prof. E. A. Spaul	1	1	0
G. M. Spooner, Esq.	1	1	0
States Committee for Fisheries, Guernsey	1	1	0
A. C. Stephen, Esq.	1	1	0
Mrs G. A. Steven	1	1	0
C. Stewart-Evison, Esq.	1	1	0
H. G. Stubbings, Esq.	1	1	0
Mrs R. S. Sturdy	1	1	0
E. J. Tabor, Esq.	1	1	0
H. E. Tabor, Esq.	1	1	0
J. M. Tabor, Esq.	1	1	0
Prof. W. M. Tattersall, D.SC.	1	1	0
Prof. G. I. Taylor, F.R.S.	1	1	0
Sir Charles Howell Thomas, K.C.B., C.M.G.	1	1	0
Sir Herbert Thompson, Bart.	1	1	0
H. Thompson, Esq., D.SC.	1	1	0
Torquay Natural History Society	1	1	0
Miss E. M. Tregoning	1	1	0
J. L. Tremblay, Esq., D.SC. (1937, 1938 and 1939)	3	3	0
G. C. Trout, Esq.	1	1	0
P. Ullyott, Esq.	1	1	0
A. M. Vardy, Esq.	1	1	0
Prof. S. L. Vella	1	1	0
Dr A. Walton	1	1	0
Sir Nicholas E. Waterhouse, K.B.E.	1	1	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
G. Weaver, Esq.	1	1	0
Miss K. M. White	1	1	0
P. H. F. White, Esq. (1937 and 1938)	2	2	0
D. P. Wilson, Esq.	1	1	0
Mrs D. P. Wilson, PH.D.	1	1	0
R. S. Wimpenny, Esq.	1	1	0
Ronald Winckworth, Esq., F.R.G.S.	1	1	0
V. C. Wynne-Edwards, Esq.	1	1	0
Prof. C. M. Yonge, D.SC.	1	1	0
John Z. Young, Esq.	1	1	0
	£313	16	0

DONATION TO THE GENERAL FUND

For the year April 1 1937 to March 31 1938

	s.	d.
Jewish Scholarship Fund	14	10
	14	10

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31 MARCH 1938

	£	s.	d.	£	s.	d.
To SALARIES, including Institution's Contributions to Superannuation				7945	15	8
„ LABORATORY WAGES, including National Insurance and Institution's Contributions to Superannuation				2498	16	3
„ DEPRECIATION OF LIBRARY				473	10	8
„ SCIENTIFIC PUBLICATIONS, *Less* SALES AND GRANT				392	0	11
„ UPKEEP OF LABORATORIES AND TANK ROOMS:						
Buildings and Machinery	434	15	1			
Electricity, Gas, Coal, Oil and Water ...	359	2	3			
Chemicals and Apparatus	406	15	6			
Rates, Taxes and Insurance	114	12	11			
Travelling Expenses	94	3	0			
Stationery, Postages, Telephone, Carriage and Sundries	356	0	4			
Specimens	107	4	6			
				1872	13	7
„ MAINTENANCE AND HIRE OF BOATS:						
Wages, including Diet Allowance, National Insurance and Casual Labour	1715	8	3			
Coal, Water, Oil, Petrol, etc.	325	2	1			
Maintenance and Repairs with Nets, Gear and Apparatus	484	6	8			
Purchase of Material for Nets for Sale, excluding Labour	468	11	1			
Boat Hire and Collecting Expenses ...	38	18	5			
Insurance	252	3	8			
				3284	10	2
„ TRANSFER TO DEPRECIATION RESERVE ACCOUNT				290	14	0
„ TRANSFER TO MACKEREL RESEARCH FUND ...				15	4	3
„ TRANSFER TO DIRECTOR'S HOUSE RECONDITIONING FUND				225	11	6
„ TRANSFER TO E. T. BROWNE—SCHOLARSHIP GRANT FUND				100	0	0
„ BALANCE, BEING SURPLUS FOR THE YEAR ...				169	10	4
				£17,268	7	4

	£	s.	d.	£	s.	d.
By GRANTS:						
Ministry of Agriculture and Fisheries Grant from Development Fund	13,204	0	8			
Fishmongers' Company	600	0	0			
British Association	50	0	0			
Royal Society	100	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee	10	0	0			
				13,994	0	8
„ SUBSCRIPTIONS (excluding Subscriptions received in advance)				305	19	3
„ DONATION—JEWISH SCHOLARSHIP FUND ...				14	10	
„ SALES:						
Specimens	1098	3	6			
Fish (*less* Expenses)	120	11	5			
Nets, Gear and Hydrographical Apparatus	615	10	9			
				1834	5	8
„ TABLE RENTS (including University of Cambridge £105; Oxford £52. 10*s*.; London £52. 10*s*.; Bristol £25; Birmingham £15. 15*s*.; Manchester £10. 10*s*.; Imperial College £10; Trustees of Ray Lankester Fund £20; Leeds £10. 10*s*.; Sheffield £10. 10*s*.)				471	11	6
„ TANK ROOM RECEIPTS				580	3	3
„ INTEREST ON INVESTMENTS, LESS TAX:						
General Fund	7	18	8			
Depreciation Fund	40	14	0			
Composition Fee Fund	2	17	6			
„ INTEREST ON BANK DEPOSIT ACCOUNT (*less* Bank Charges)	1	4	8			
				52	14	10
„ SALE OF DR M. V. LEBOUR'S BOOK				4	15	4
„ SALE OF "MARINE FAUNA OF PLYMOUTH" ...				6	19	0
„ INCOME TAX RECOVERABLE				17	3	0
				£17,268	7	4

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31 MARCH 1938

	£ s. d.	£ s. d.	£ s. d.
SUNDRY CREDITORS:			
On Open Account			650 9 1
PROPORTION OF SUBSCRIPTIONS RECEIVED IN ADVANCE			136 19 9
JEWISH SCHOLARSHIP FUND:			
As at March 31 1937		14 10	
Add: Fifth Instalment received		62 1 8	
Grant received		35 2 6	
	£ s. d.	97 19 0	
Less: Expenditure	97 4 2		
Donation transferred to Income and Expenditure Account	14 10	97 19 0	– – –
E. T. BROWNE—SCHOLARSHIP GRANT FUND:			
As at March 31 1937		132 8 4	
Interest on Bank Deposit		7 10	
Transfer from Income and Expenditure Account		100 0 0	
		232 16 2	
Less: Expenditure		208 16 0	24 0 2
AQUARIUM GUIDE PRINTING FUND:			
As at March 31 1937		20 0 0	
Sale of Aquarium Guides		8 4 6	
		28 4 6	
Less: Expenditure		1 10 0	26 14 6
DR H. B. MOORE—SPECIAL GRANT FUND:			
Grant received		175 0 0	
Less: Expenditure		175 0 0	– – –

	£ s. d.	£ s. d.
BOATS AND EQUIPMENT, as per Valuation as estimated by the Director at March 31 1931		
S.S. *Salpa*	2000 0 0	
Motor Boat	150 0 0	
Nets, Gear and General Equipment	27 0 0	2177 0 0
LABORATORY APPARATUS, ENGINES AND PUMPS:		
As per Valuation as estimated by the Director at March 31 1931, plus additions at Cost		
As at March 31 1937	1023 2 5	
Additions during the year (Net)	127 4 0	1150 6 5
LIBRARY:		
As per Valuation as estimated by the Director at March 31 1931, plus additions at Cost, *less* Depreciation		
As at March 31 1937	2277 2 4	
Additions during the year	491 13 3	
	2768 15 7	
Less: Depreciation	473 10 8	2295 4 11
STOCK OF SPECIMENS, CHEMICALS AND JOURNALS:		
As estimated by the Director		510 0 0
SUNDRY DEBTORS:		
Sale of Specimens, Journals, Nets, Gear and Apparatus		187 7 6
INCOME TAX RECOVERABLE		39 1 11
PREPAYMENTS		114 9 11
GENERAL FUND INVESTMENT at Market Value as at March 31 1931:		
£352. 2*s.* 3*d.* Local Loans 3% ... ... (Market value at date £302. 16*s.* 4*d.*)		232 7 10

MACKEREL RESEARCH FUND:						
As at March 31 1937	56	11	11			
Grant received	543	8	1			
Transfer from Income and Expenditure Account	15	4	3			
	615	4	3			
Less: Expenditure	615	4	3			
				–	–	–
RESERVE FOR DEPRECIATION OF BOATS AND MACHINERY:						
As at March 31 1937	1744	6	7			
Add: Transfer from Income and Expenditure Account	290	14	0			
				2035	0	7
COMPOSITION FEE FUND:						
As at March 31 1937				126	0	0
CONSTANT TEMPERATURE ROOMS FUND:						
Special Donations received	800	0	0			
Less: Expenditure	666	15	4			
				133	4	8
DIRECTOR'S HOUSE RECONDITIONING FUND:						
Grant received	350	0	0			
Transfer from Income and Expenditure Account	225	11	6			
	575	11	6			
Less: Expenditure	575	11	6			
				–	–	–
SURPLUS:						
As at March 31 1937	6152	16	3			
Add: Surplus for the year as per Income and Expenditure Account	169	10	4			
				6322	6	7
				£9454	15	4

DEPRECIATION FUND INVESTMENTS at Cost:						
£590. 6*s.* Local Loans 3%	506	10	9			
£1502. 1*s.* 10*d.* Conversion Loan 3%	1528	9	10			
(Market value at date £2017. 5*s.* 2*d.*)				2035	0	7
COMPOSITION FUND INVESTMENTS at Cost:						
£18. 8*s.* 6*d.* Local Loans 3%	15	15	0			
£108. 6*s.* 5*d.* Conversion Loan 3%	110	5	0			
(Market value at date £124. 14*s.* 2*d.*)				126	0	0
CASH AT BANK AND IN HAND:						
Coutts & Company—Current Account	476	10	6			
Lloyds Bank Limited—Current Account ...	169	7	8			
Cash in Hand	41	18	1			
	687	16	3			
Less: Coutts & Company—Loan Account E. T. Browne—Scholarship Grant Fund	100	0	0			
				587	16	3
				£9454	15	4

E. J. ALLEN }
M. BURTON } *Members of Council.*

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the Association and have obtained all the information and explanations we have required. Capital expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs according to the best of our information and the explanations given to us and as shown by the books of the Association.

34 *and* 35 *Bedford Street,*
Plymouth. April 20 1938

PRICE, WATERHOUSE AND CO.

OBSERVATIONS ON THE BIOLOGY AND POST-EMBRYONIC DEVELOPMENT OF *IDOTEA VIRIDIS* (SLABBER) (ISOPODA, VALVIFERA) FROM NEW ENGLAND CREEK, SOUTH-EAST ESSEX

By N. H. Howes, M.Sc.

Department of Zoology and Comparative Anatomy,
University College, University of London

(Text-figs. 1–14)

CONTENTS

	PAGE
Introduction	279
Methods and nomenclature	280
The adult *Idotea viridis* (Slabber) from New England Creek	281
Seasonal changes in numbers	287
Number of young in brood pouch	290
The newly hatched *I. viridis*	292
The ecdyses between hatching and maturity	294
Changes in bodily form	296
Allometry	297
Changes in shape	301
Discussion	304
Summary	309
References	310

INTRODUCTION

In the course of an ecological survey of a saline lagoon, New England Creek in south-east Essex (Howes, 1939), it was found that one of the dominant species of animals present was a form, possibly a local race, of *Idotea viridis*. New England Creek runs from the Yokefleet, a branch of the River Roach, on to the Maplin Sands. It was dammed at both ends in 1925 while still full of water, and by 1934 had become a lagoon containing approximately 250,000 cu. m. of water of lower salinity than, and of a slightly different composition from, sea water (Howes, 1939). The lagoon was visited at regular intervals, usually about every four weeks, throughout 1934, 1935 and 1936, samples of the water being taken for analysis and specimens of the fauna collected at each visit. Further, a standard haul was made with a plankton net on each occasion. The *I. viridis* proved to be an active swimmer and, apart from specimens collected by hand, over eight thousand in all were taken in the plankton alone. Thus a collection was made which included all stages in the post-embryonic development of this species and, since it was well preserved, provided excellent material for studying its biology.

The species *I. viridis* appears to contain animals showing a wide range of morphological variation, especially between individuals collected from different localities, i.e. there appear to be well-defined local races of which the New England Creek form may be one. Since the latter does not exactly tally with the earlier accounts of *I. viridis*, a detailed description was deemed advisable before discussing its biology. After this description, the paper deals first with the annual change in numbers of *I. viridis*, the number of eggs in the brood pouch and the distribution of different size groups in the plankton hauls throughout 1936. The nature of these phenomena may be peculiar to this race. Following this, the newly hatched animal is described, and then the change in shape of the body, the coxal plates and of certain appendages, as the animal develops into the adult. Although the material suffers from being derived from a form of *I. viridis* that may not be common in England, which may, indeed, be confined to the lagoon, New England Creek and to dykes draining into that creek, nevertheless it is believed that the results of this latter investigation recorded below are, in a modified degree, applicable to the Idoteidae as a whole. Idoteids appear rarely to be found together in large numbers, and a series of individuals, representing every instar from hatching to maturity, is so difficult to obtain that little is known of their development.

METHODS AND NOMENCLATURE

The animals were collected by hand and with nets, the majority with a plankton net. They were then killed and fixed by the addition of sufficient formalin to the water in which they were, to produce a final concentration of approximately 5 %. Fixed animals were used for all measurements recorded. The animal was placed on a well slide in water, lightly pressed flat by means of a cover-slip or piece of slide, lighted from above and measured to the nearest $\frac{1}{100}$ mm. by means of a travelling microscope at a magnification of 20 diameters; for animals of the first and second instars, an eyepiece micrometer was substituted for the travelling microscope. Apart from errors inherent in the method owing to distortion on fixation, measurements made of the same animal on different occasions showed that an accuracy of well within ±2 % was usually attained.

For morphological studies, animals or appendages were mounted untreated in Canada balsam or Gurr's water mounting medium: specimens were also heated over a boiling water bath in 2 % caustic soda and the chitinous skeleton obtained then mounted in Canada balsam. In regard to the nomenclature of the three main divisions of the body, I have followed Calman (1909) since there seems to be no reason to suppose that they are other than homologous with the corresponding regions of the Malacostraca as a whole, and have called them, cephalon, thorax and abdomen, discarding the arachnidan terms used by Sars (1899) and Collinge (1917), namely cephalon, mesosome and metasome, respectively. Following the nomenclature customary in Isopoda, the first free thoracic segment is referred to as the first thoracic segment and the remaining segments numbered accordingly. Needham (1937), to whose work considerable reference is made, calls the first *free* thoracic somite the second thoracic segment. In the light of more recent work, Collinge's "lateral clefts" of the cephalon are referred to as "occipital grooves" and that part of the cephalon lying behind them as the "maxillipedal somite" (Jackson, 1926). The names of the joints of the maxillipedes are taken from Hansen (1925), the lateral half of Collinge's (1918) divided coxopodite then becoming the proximal epipodite and the median half the coxa proper. The use of the term "fused dactylus and carpo-propus" for the distal joint of the maxillipedal palp may be quite unjustified, but since it was necessary to refer to individual joints by name, I have taken the liberty of thus modifying Hansen's description of the maxillipede of *Glyptonotus*; it is not claimed that this is a correct homology, but the knee is definitely situated between the two distal joints in the species described above. All the illustrations in this paper are made from individual specimens and no attempt has been made to produce generalized diagrams, hence slight variations in shape are to be expected. It should be noticed that there are considerable variations in size in each instar.

THE ADULT *IDOTEA VIRIDIS* (SLABBER) FROM NEW ENGLAND CREEK

Body narrow, elongated (Fig. 1), about 4·6 times as long as broad; dorsal surface moderately convex, surface either smooth or pitted. *Cephalon* (Fig. 2*a*) wider than long, ratio breadth/length, males 1·45 ± 0·12 (120 specimens), females 1·48 ± 0·12 (45 specimens); anterior margin slightly emarginate, posterior margin straight; lateral margin with slight fissure at point of demarcation of the maxillipedal somite from rest of cephalon; fissure continued as strongly-marked occipital groove, extending one-quarter of width of cephalon inwards, not visible in mid-line; maxillipedal somite about one-fifth length of cephalon, lateral borders tapering to an antero-lateral blunt point faintly divided by groove. Eyes large, length about one-third cephalon, situated dorso-laterally, posterior margin on median transverse line of cephalon. *Antennulae* (Fig. 2*b*) extending well beyond third peduncular joint of antenna, first joint expanded, irregularly angular, second joint nearly as long but narrower, third joint slightly elongated; flagellum (Fig. 2*c*) single-jointed, clavate, lateral angle acute, antero-medial surface rounded with three or four setae and eight (one isolated lateral, three pairs and one single median) spindle-shaped, pedunculate aesthetascs (Fig. 2*d*), each with truncate distal tip where pore opens to exterior. *Antennae* (Fig. 2*e*) elongated, first peduncular joint very short, with dorsal forwardly directed rounded angle, second longer, incised laterally with dorsal forwardly directed obtuse point, third scarcely longer than second, concave distally on both dorsal and ventral surfaces with median and lateral anterior projections, fourth longer than third with dorsal forwardly directed obtuse point and single antero-lateral spine, fifth joint longer and narrower than fourth; flagellum about one and a quarter times length of peduncle with 11 to 13 joints in fully grown males, first joint somewhat elongated, terminal style (Fig. 2*f*) almost cylindrical, half length of preceding segment. *Maxillulae* (Fig. 2*g*, *h*): outer lobe terminating in eleven curved spines, six outer (four or five toothed), five inner (three toothed, two median slender and untoothed); inner lobe terminally rounded with three setose spines and small outer spine. *Maxillae* (Fig. 2*j*) consisting of two laminar setose lobes, outer bipartite lobe with long ctenate setae, inner lobe with row of setae, three innermost slightly stouter and markedly plumose. *Maxilli-*

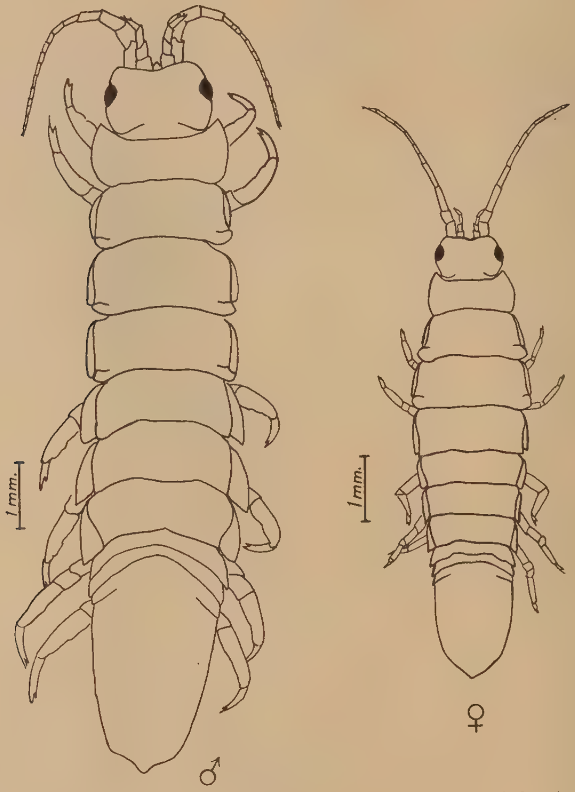


Fig. 1. Adult male and female of *Idotea viridis* (New England Creek, Essex).

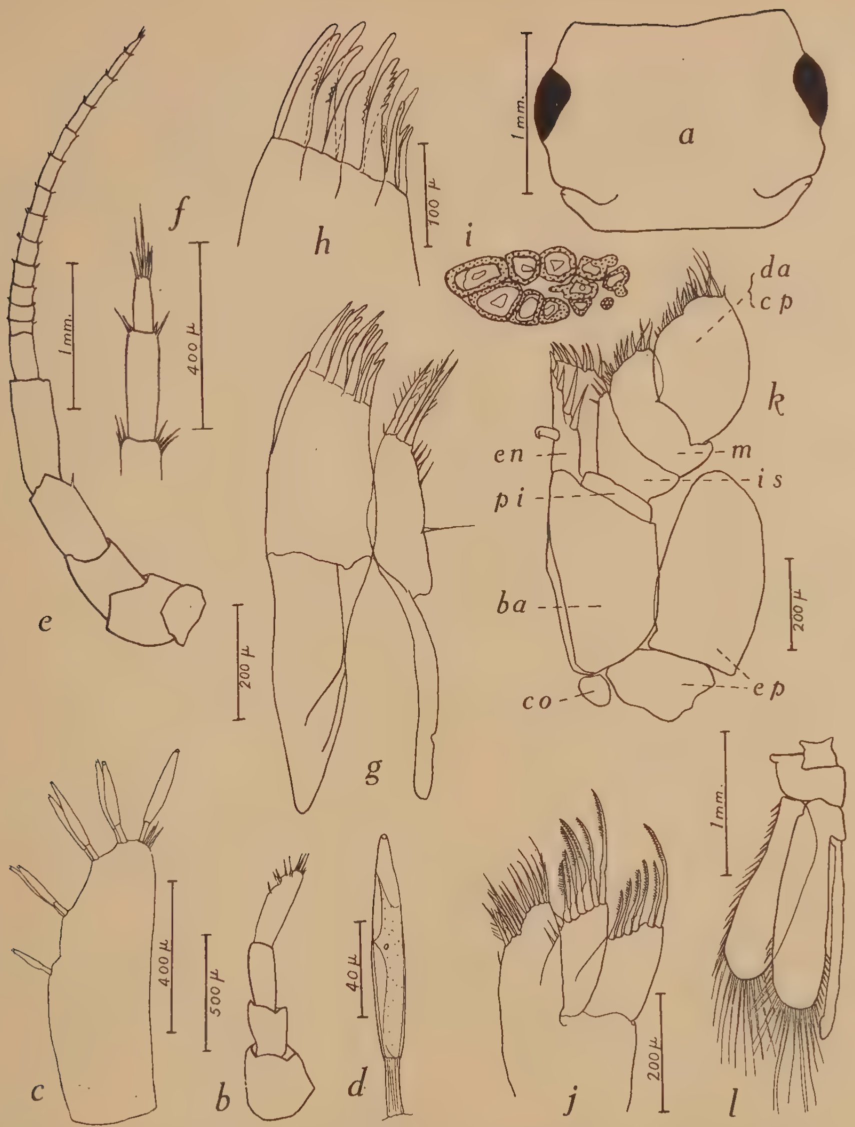


Fig. 2. *Idotea viridis* (New England Creek, Essex). *a*, cephalon, dorsal view, 12·5 mm. ♂; *b*, right antennula, dorsal view, 11 mm. ♂; *c*, flagellum of right antennula, artificially flattened to show distribution of aesthetascs; *d*, aesthetasc; *e*, right antenna, dorsal view, 11 mm. ♂; *f*, terminal setose style of right antenna; *g*, right maxillula, ventral view, 13 mm. ♂; *h*, tip of outer lobe of right maxillula; *i*, oblique section through maxillula passing transversely through bases of spines, inner side of lobe to the right, dorsal surface at top; *j*, left maxilla, ventral view, 13 mm. ♂; *k*, right maxillipede, ventral view, 13 mm. ♂; *ba*, basis; *co*, coxa; *cp*, *da*, carpo-propus, dactylus; *en*, endite; *ep*, epipodites; *is*, ischium; *m*, merus; *pi*, preischium; *l* ,second right pleopod, ventral view, 14 mm. ♂. (In all cases the appendages are described in their *anatomical* position.)

pedes (Fig. 2*k*) with four-jointed palp, distal joint of palp with marked nick on inner margin, pre-ischium rectangular when viewed from above; basis large, nearly as long as palp; size ratio of coxa and proximal epipodite variable; tip of endite slightly more than half way up inner border of merus, inner border bent dorsally, hence endite roughly L-shaped in cross-section, with single coupling hook projecting inwards at angle; width of dorsally-directed portion half of transverse flattened region. First, fifth, sixth and seventh segments of *thorax* (Fig. 1) shorter than second, third and fourth; first shortest and seventh scarcely longer; segments two, three and four approximately same length; segments increasing slightly in width up to segments five and six, segment seven narrower again; anterior angles of pleuron of first thoracic segment sharply pointed, projecting laterally beyond borders of head and forward well anterior to occipital groove; in adult males this segment about 20 % wider than cephalon. Coxal plates (Fig. 3*e*, *f*) in two groups, those of segments two, three and four showing only a narrow projection beyond lateral pleural margin, occupying from under three-quarters to over nine-tenths respectively of lateral margins of segments, visible right up to and round antero-lateral angles; coxal plates of segments five, six and seven wide, almost triangular, projecting well beyond lateral borders of segment throughout length; coxal plate of segment seven with backwardly projecting acute angle. In segments two, three and four, a small area of pleuron separated from rest by a medially directed transverse slit visible from below; in segments two and three remains of pleuron projecting to lateral border of coxal plates, separated from latter by slight nick; in segment four ending more medially and in segment five scarcely visible. Remaining thoracic appendages (Fig. 3*a*, *b*) similar to those of other members of genus. *Abdomen* (Figs. 1, 3*d*) with two short segments and antero-transverse grooves indicating coalesced third, forming about 33·5 % of total body length (anterior border of cephalon to posterior tip of abdomen); terminal fused segment moderately long, 84 % of total abdomen length; total abdomen in intact animal about 1·9 times as long as wide; posterior margin convex with single median tooth and lateral corners forming an angle of about 110°. *Appendix masculinus* of *second pleopods* (Fig. 2*l*) extending well beyond end of endopodite. *Uropoda* (Fig. 3*c*) flattened, elongated, rounded anteriorly, slightly broader in middle than at ends, endopodite obtusely truncated; setose style arising from basal plate reaches to tip of endopodite.

Length of animal: adult males, 12–14 mm.; ovigerous females, 5·5–10·5 mm.

Colour: background generally brown, but not rarely white or with white patches, with variously distributed melanophores giving a large range of different patterns, most commonly with an even distribution. Background remains brown in alcohol.

Distribution: New England Creek and dykes draining into it, near Great Wakering, south-east Essex. This environment has been described in some detail elsewhere (Howes, 1939). The species is very common indeed and it is calculated that the creek contains of the order of two and a quarter million individuals when peak numbers are present (Fig. 4).

It is strange that no reference is anywhere made to the fact that the endite of the maxillipede is bent upwards so as to have the inner surfaces in both a horizontal and a vertical plane, thus making the joint L-shaped or triangular in cross-section, with the coupling hook arising from the angle thus made. This condition is probably widespread in the Idoteidae and certainly occurs in *I. baltica*, *I. neglecta*, *I. emarginata*, *I. granulosa*, and *I. linearis*, although often to a much less marked degree than in *I. viridis*.

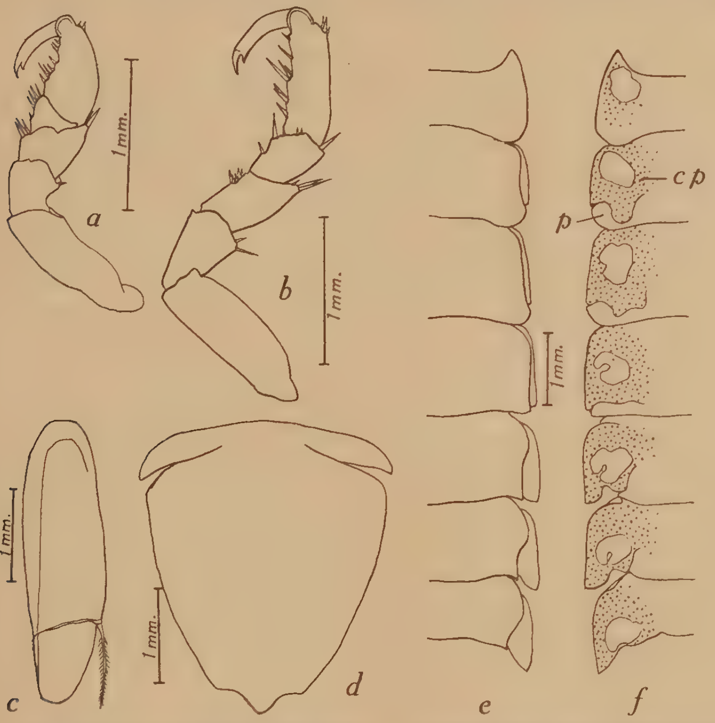


Fig. 3. *Idotea viridis* (New England Creek, Essex). *a*, anterior view of first pereiopod, 11 mm. ♂; *b*, anterior view of seventh pereiopod, 11 mm. ♂; *c*, left uropod, ventral, of 12 mm. ♂; *d*, dorsal view of fused segments of abdomen of 12 mm. ♂ (prepared by dissecting out pleopods and soft tissues and pressing abdomen flat); *e*, dorsal view, *f*, ventral view, of coxal plates of 13·4 mm. ♂ (preparations made after treatment with caustic soda. Ventral view, coxal plates are dotted); *cp*, coxal plate; *p*, pleuron. (In all cases the appendages are described in their *anatomical* position.)

The aesthetascs of the antennules do not seem to have been observed, but experience has shown that they have the appearance of setae when the appendage is mounted in either Canada balsam or in water mounting medium;

and in marine forms they are often so covered by ectoparasitic Peritrichida as to be completely obscured. In water their structure can more easily be made out and it was possible to study them in some detail in the *I. viridis* from New England Creek, where they were scarcely ever parasitized. They closely resemble the "olfactory setae" or "Riechstäbchen" described by Scourfield (1896, 1905) in Cladocera and other forms, being shaped like those of, e.g., *Daphnia magna*, except that they are not divided transversely and are stalked. They resemble those of *Asellus aquaticus* in being divided into a hyaline distal portion and a proximal stalk with strongly chitinized walls. These aesthetascs have been examined both with ultra-violet and red and blue light under critical conditions and in the position occupied by the "terminal pellet" on the aesthetascs of Cladocera (Scourfield, 1905) there is in this species a tiny open pore. The arrangement of the aesthetascs on the flagellum of the antennule might prove to be a useful secondary systematic character, since, if fully grown animals were compared, it was found to be constant. It suffers from the disadvantages that the organs are very liable to be parasitized and that the number and arrangement alters from instar to instar.

Idotea viridis *from New England Creek compared with* I. viridis (*Slabber*) *as described by Sars* (1899)

Body form somewhat more slender, cephalon wider, frontal margin similar. Eyes appear larger. Antennule similar. Joints of antennary peduncle differing in detail, proximal joints of flagellum shorter and style of flagellum shorter in proportion to penultimate segment. Coxal plates only occupying anterior three-quarters of lateral margins of segments two, three and four and not reaching posterior margin of segment five. Legs similar, joints of P 1 about 25 % broader in proportion to length, P 7 carpus markedly shorter than merus, again broader in proportion to length. Abdomen similar. Stylet of pleopod 2 projecting to a similar extent. Endopodite of uropod more tapering; tip of setose style level with posterior end of uropod.

I. viridis *from New England Creek compared with* I. viridis (*Slabber*) *as described by Collinge* (1917)

Body shape similar, cephalon proportionately wider, eyes larger. Basal joints of antennules differing in shape and proportions. Antennae: style shorter. Maxillulae: eleven spines (seven or eight, toothed) instead of nine (three, toothed). Characteristically, two median spines slender and untoothed. Except for first, segments of thorax almost equal in length. Coxal plates of segments two, three and four similar but narrower, of segments five, six and seven not contiguous and narrower. Maxillipedes similar; other thoracic appendages, P 1 slightly stouter in proportion, propus of P 7 very much stouter, carpus shorter than merus. Abdomen similar. Endopodite of uropod more tapering, setose style reaching posterior tip of endopodite.

It thus appears that *I. viridis* from New England Creek differs from those described by Sars and by Collinge in many particulars, especially in the size of the eyes, the shape of the style of the antenna, the size of the coxal plates as measured by the lateral expansions visible from the dorsal surface, the build of the peraeopods, the shape of the endopodite of the uropod and the length of the setose style. It further differs from Collinge's description in that the outer lobe of the maxilla terminates in eleven spines instead of nine. But these are characters which appear to vary more or less independently of each other throughout the species. Mr G. M. Spooner kindly lent me his collection of *I. viridis*, which contained specimens from nine different localities, six in the Tamar Estuary, two near Weymouth and one from Holbeach on the Wash, and my collection includes animals from three different habitats near Great Wakering, Essex. On the whole, animals obtained from the same locality closely resemble one another, apart from age and sex differences, but may differ from the *I. viridis* described by Sars, by Collinge or that from New England Creek in some or all of the characters enumerated above, except that every adult male from the two collections had eleven spines on the outer lobe of the maxilla. This last character is not likely to prove of diagnostic value since it occurs commonly throughout the genus (Collinge, 1917).

There remain three characters which serve to differentiate the species *viridis* from other members of the genus *Idotea* and yet include in that species the animals described by Sars and by Collinge as *I. viridis*, together with the twelve forms mentioned above. These are, in the adult male: (*a*) body slimly built, with lateral margins almost parallel and with the widest region in the fifth and sixth thoracic segments rather than in the third or fourth as in other species; (*b*) cephalon with overall breadth only about 1·5 times overall length; (*c*) abdomen slightly tapering posteriorly, terminating in a single median tooth; obtuse postero-lateral corners very distinctly marked but never projecting backwards as lateral teeth.

This scheme closely follows the points stressed by Sars (1899, p. 84) and it is the basis upon which the *Idotea* collected in New England Creek are considered to be *I. viridis*.

Seasonal Changes in Numbers

New England Creek runs from the Yokefleet, a branch of the River Roach, on to the Maplin Sands. It was dammed in 1925 and a body of water was enclosed with the intention of draining the creek later on. This has not been done, but the salinity of the water has become reduced and a great many chemical changes have taken place. A fairly detailed study of these changes and of the fauna and flora has been made and is published elsewhere (Howes, 1939). The creek in 1934–6 was about $1\frac{1}{2}$ miles long, had a maximum depth of $3\frac{1}{2}$ m. and a surface area of 144,000–170,000 sq. m., and contained between

230,000 and 299,000 cu. m. of water. The predominant plant species were *Ruppia maritima* and *Chaetomorpha linum*, the former occurring in large quantities and reaching the surface.

Idotea viridis was very common, and was found swimming and crawling on the stems of *Ruppia*. Observations suggest that it eats polyps of *Membranipora* and of coelenterates, though any dead animal in the creek always had a large number of specimens crawling on it. In cold weather the numbers of *Idotea viridis* appear to be very much reduced and only a few specimens can be found crawling in weed near the bottom.

The creek was visited once every four weeks, and on each visit a haul was made with a silk plankton net, 100 strands to 1 in., over a measured length of 1325 m. Details of this haul and a discussion of its value as a quantitative method are given in an earlier paper (Howes, 1939) and it suffices here to state that approximately 100 cu. m. of water were filtered. At the completion of each haul, not only were the contents of the bucket preserved, but the silk was carefully examined, all visible adhering organisms removed with a camel hair brush and added to the catch in the bucket. The number in each catch represents both swimming animals and others swept off surface weed by the net. Results obtained by counting the number of *Idotea* in each catch for the years 1934, 1935, 1936 are given in Fig. 4.

The interest of this diagram lies in the paucity in numbers of *I. viridis* in the first five months of the year, the very rapid rise to a maximum in late June and in July and the way in which the numbers remain comparatively high until the end of October, then fall off rapidly, rising again in December. It is believed that the lateness of the attainment of maximum numbers is mainly due to the carnivorous nature of the New England Creek race and that no considerable reproduction occurs until a plentiful supply of coelenterates and especially of *Membranipora crustulenta* var. *fossaria* is available. Observation has shown that these forms become common about May and that the *Membranipora*, at least, continues to be present in quantity until October. The significance of the rise in December is not understood. The method of collecting nekton forms by means of a plankton net towed just below the surface is obviously open to criticism and it is important to enquire how far the picture presented by these data really represents the behaviour of the population in the creek. It is known that all sizes of *Idotea*, including ovigerous females, are taken in the hauls (Fig. 5), so that the result cannot be entirely due to certain instars retiring beyond the reach of the net. Further, a visit to the creek in late summer or early autumn impresses one with the extraordinary plentifulness of *I. viridis*; on the other hand, in late winter or early spring it is possible to spend a whole day collecting and not see a single specimen unless they are very specially looked for; even dragging weed from the depths will only yield an occasional individual. It can therefore be concluded that Fig. 4 is a fair rough representation of the behaviour of the population as a whole. It can be calculated that at the peak periods in 1934 and 1936 the

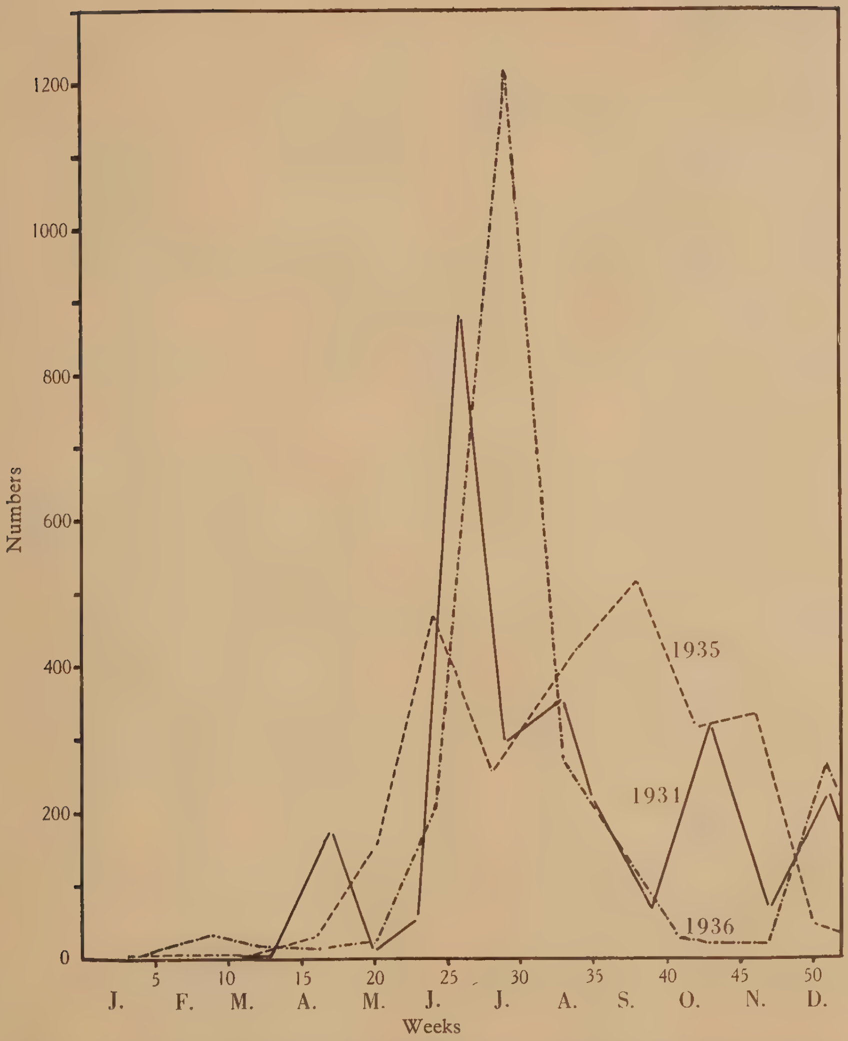


Fig. 4. Curves showing the annual change in numbers of *Idotea viridis* (all sizes) in 100 cu. m. of water, from New England Creek, Essex, for the years 1934, 1935 and 1936, in which the totals were 2656, 2339 and 3127 respectively. (—— 1934; – – – 1935; – · – · – 1936.)

total number of *I. viridis* in New England Creek was of the order of two and a quarter million.

All the idoteids collected in 1936 were measured and have been segregated into size groups, which do not represent instars. These results are shown in Fig. 5. It will be seen that newly hatched individuals (1·50–1·99 mm. long) first appear in May, reach their maximum in July, disappear in October and November and reappear in small numbers in December, suggesting that *I. viridis* has a second late brood, as do many marine plankton forms; the figure also shows that animals between 2·00 and 5·99 mm. in length represent the greater part of the plankton collections. This is taken to mean that there is a considerable mortality of young forms, especially at that ecdysis which precedes sexual maturity (Table I) and possibly that the older forms tend to some extent to remain nearer the bottom. For the reasons presented above, it is not considered that this latter factor involves any fundamental alteration in the data presented in Fig. 4.

Number of Young in Brood Pouch

In order to determine the fertility of *I. viridis*, the numbers of embryos in the brood pouches were counted. Preliminary investigation showed that if ovigerous females were selected as such from a collection, there was always a tendency to choose those containing large numbers of eggs, hence every female collected in 1935 and 1936 has been examined and, if ovigerous, the embryos have been removed from the brood pouch and counted. The embryos have been divided into three groups, (*a*) the spherical or semi-spherical, referred to as "eggs", (*b*) those shaped as an oblate spheroid and with obvious mesodermal bands, "medium", and (*c*) those with appendages, "advanced". The results of counts made on 121 ovigerous females are shown in Fig. 6.

It would clearly be most misleading to express these results in terms of an average number of eggs per female, since there is a large number (41) of females whose brood-pouch contained 1–6 embryos, mostly in the "advanced" stage, and the remaining females fall, with six exceptions, into four main groups, containing round about 9, 13, 17 and 23 embryos respectively. The exceptional animals had 26, 31, 33, 34 and 46 embryos. There is some tendency for the "advanced" stages to be grouped on the left, i.e. for there to be few animals of this stage in the brood-pouch and for the "eggs" to be on the right. The data available do not justify an attempt fully to explain these facts, but they may be partially accounted for. Observations show that there is some difference in the stage of development of embryos within the marsupium, e.g. while the majority are ready to hatch, three or four may be at an earlier stage. It is possible that these latter may be retained after the others have left the pouch, in this way accounting for the females with 2–6 embryos. Jancke (1924) showed that in *Asellus aquaticus*, the number of fertilized eggs was twice reduced by expulsion, first, of early embryos and later, of more

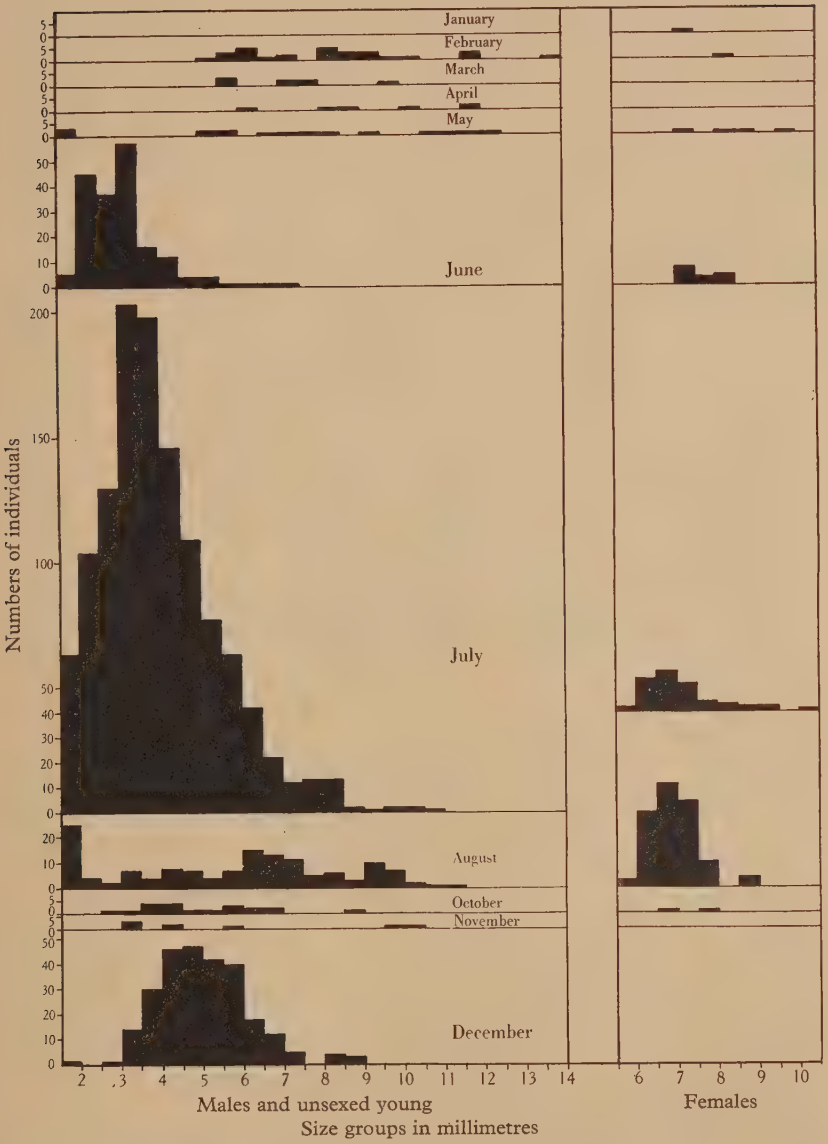


Fig. 5. Size-composition of plankton catches of *Idotea viridis* in New England Creek throughout 1936.

developed embryos; 150 fertilized eggs eventually giving rise to a brood of about 8. He also observed a similar phenomenon in *Idotea viridis*, according to Zimmer (1927), viz. a reduction of 30–40 eggs to 4–6 young ready to hatch. The decrease in "advanced" and "medium" embryos from left to right in the figure suggests the possibility that a similar process also takes place in *I. viridis* in New England Creek. Females with only one embryo in the marsupium occurred only in August and September; it is not known whether this is again part of the phenomenon discussed above, or whether the embryo was retained in the pouch, there to pass the winter. The grouping of the remaining females is not correlated either with size of mother or with the season: it is possible that a genetical factor may be operating.

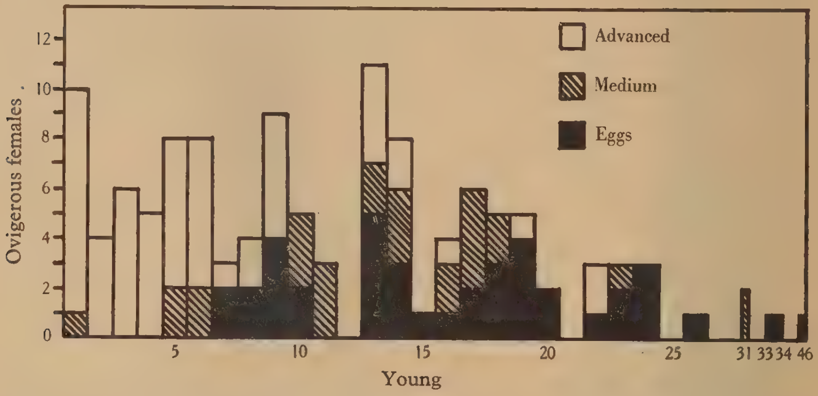


Fig. 6. Diagram showing variation in number of young in brood pouch of ovigerous *Idotea viridis*. The base line is divided into number of young in brood pouch and the values of the ordinates are proportional to the number of females containing a given number of eggs. The young are grouped into "eggs", "medium" and "advanced". The four columns on the right, which are half the width of the other columns, represent animals with exceptionally large numbers of young in the brood pouch. The total number of females was 121.

THE NEWLY HATCHED *IDOTEA VIRIDIS*

The material upon which this description is based was collected in the plankton, but the fact that these really were newly hatched animals was confirmed by examination of young from brood-pouches.

I. viridis, when just hatched (Fig. 7*a*), is between 1·5 and 2·4 mm. long, mean length 1·8 mm. Cephalon relatively enormous, body tapering posteriorly. Flagellum of antennule consisting of two segments. Thorax of six large segments each bearing a pair of legs and one limbless posterior small segment; this is characteristic of all isopod young at this stage (Calman, 1909). Coxal plates relatively broad, visible on all thoracic segments including first and rudimentary seventh; convex laterally, large and very conspicuous on thoracic

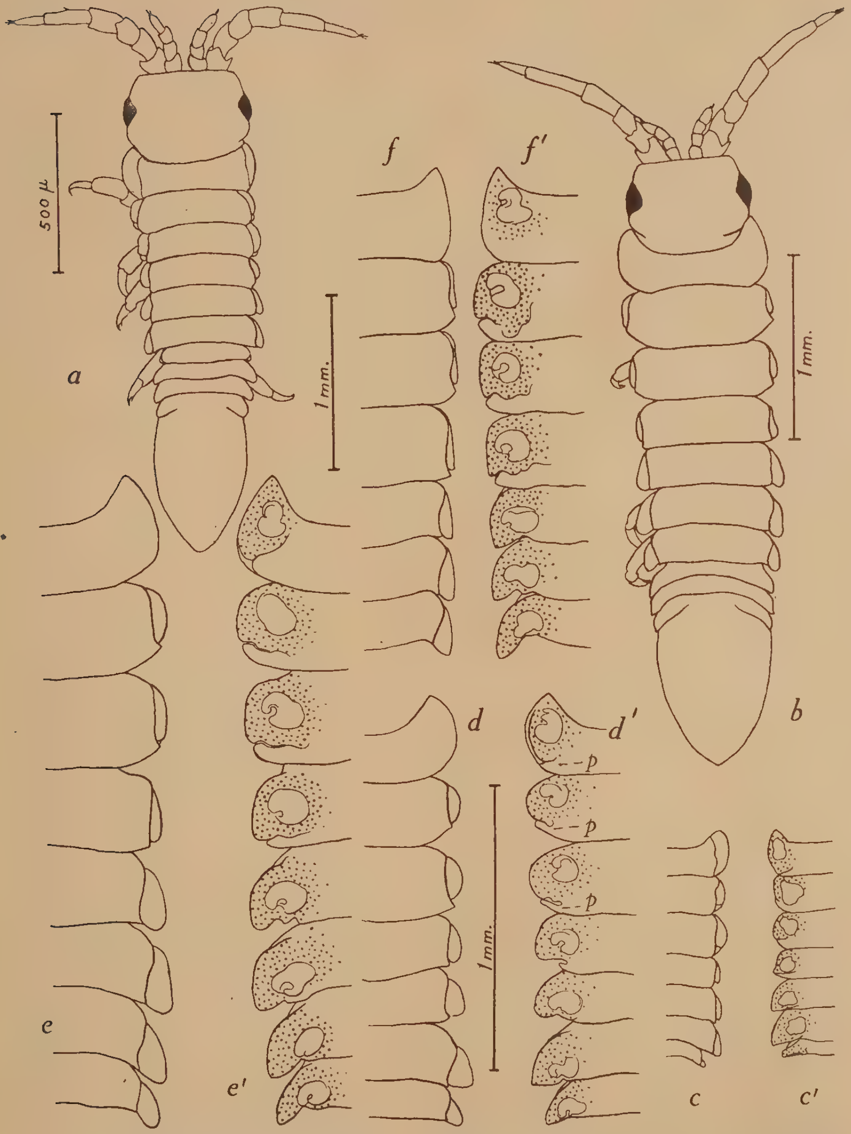

500 μ
1 mm.
1 mm.
1 mm.
a
b
c
c′
d
d′
e
e′
f
f′
p
p
p

Fig. 7. *a*, newly hatched *Idotea viridis*; *b*, *I. viridis* in instar II; *c*, *c′*, *d*, *d′*, *e*, *e′*, dorsal and ventral views respectively of coxal plates in instars I, II and III (all drawn to the same scale); *f*, *f′*, dorsal and ventral views of coxal plates of instar IV; *p*, pleuron.

segment one, diminishing in size to segment six, minute on segment seven. Abdomen with two short segments and antero-transverse groove indicating coalesced third, as in adult.

THE ECDYSES BETWEEN HATCHING AND MATURITY

Several attempt at rearing *I. viridis* from New England Creek in the laboratory were made, but, although adults lived for some weeks in captivity, they all died without growing or producing young, probably because it was impossible to maintain supplies of suitable food. Hence it was necessary to try to determine the number of ecdyses from the preserved material. It was found that if the animals were classified according to the number of joints of the flagellum of the antenna, there was marked correlation between this quantity and the length of the animal, but with considerable overlapping in size between adjacent classes and, in certain cases, e.g. forms with eight, nine and ten joints, almost complete overlap. Where the length of a number of animals extended over the same range, even if there were differences in the number of joints of the flagellum, they were taken as one class. It was then found that these classes could be arranged serially so that each group represented a different instar, saving that the first group included animals covering an exceptionally wide size range and with obvious morphological differences. This group will be dealt with later. That the other groups did, in fact, represent instars, was confirmed as follows: all the animals in a group were examined and those about to moult, i.e. with the skeleton of the coming instar visible inside the existing skeleton, were segregated. The new antennae could be seen inside the old antennae of these forms and hence the coming

TABLE I. INSTARS OF *I. VIRIDIS*

Ratio of mean lengths of animals in instar to that of animals in preceding instar "Przibram quotient"	Instar no.	Number of segments in flagellum of antenna	Mean length of animals in instar mm.	Limits of length of animals in instar mm.	Notes
	1	2	1·8	1·5–2·4	Newly hatched
1·44	2	2	2·6	2·1–3·6	
1·38	3	3	3·6	3·0–4·5	
1·25	4	4 or 5	4·5	3·8–5·6	
1·31	5	6 or 7	5·9	4·9–7·5	At this stage some ♀♀ become mature
1·26	6	8, 9 or 10	7·4	6·1–8·5	At this stage rest of ♀♀ become mature, ♂♂ have *appendix masculinus*
1·36	7	11, 12 or 13	10·1	8·4–12·7	Males show sudden widening of 6th thoracic segment

change in the number of joints determined; it was found that the smallest animals in group one, which had only six thoracic peraeopods, could have the same number (two) of segments in the flagellum in the following, as in the present, instar. This group was therefore separated into instars on the basis of the number of thoracic legs. It could be seen that animals of the second instar added one joint to the flagellum; of the third, one or two; fourth, one or two; fifth and sixth, two or three (Fig. 8): on this basis Table I was constructed.

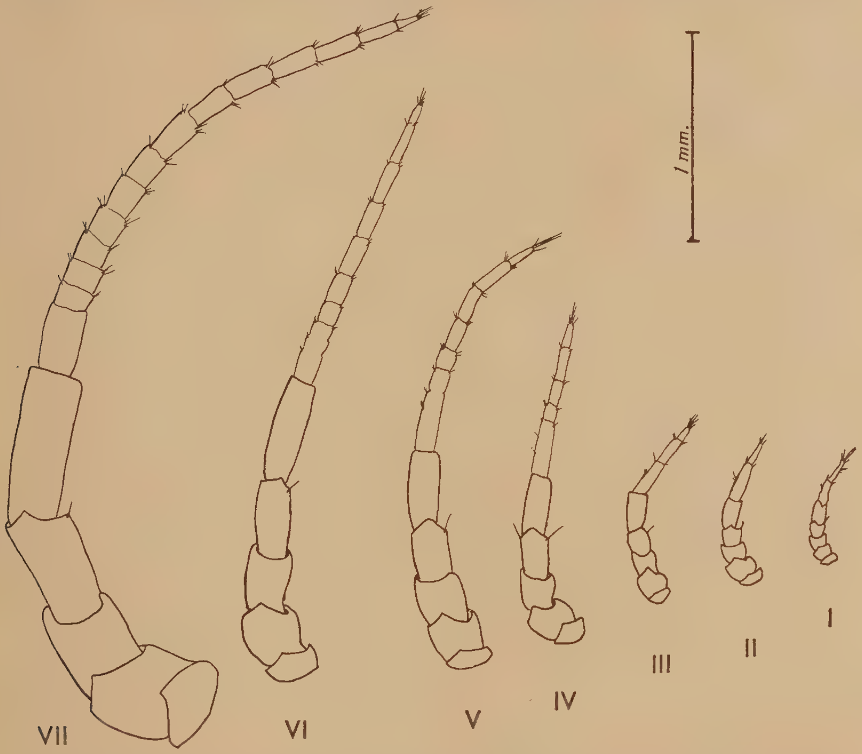


Fig. 8. Antennae of different instars of *Idotea viridis* showing increase in number of joints of flagellum. Newly hatched animal on right. The numbers below the appendages indicate the instar to which the animal belongs.

The lengths of twenty animals in each instar were measured; results so obtained are given in the table.

Normally there are six moults after hatching before the male *I. viridis* from New England Creek stops growing, and rarely there may be a seventh, after which the animal has fourteen or fifteen joints on the flagellum of the antenna and reaches a length of nearly 14 mm. Animals of this size were extremely rare. Usually, in the sixth instar the male has the *appendix masculinus* of the 2nd pleopod in the adult condition; females appear to become ovigerous in the fifth instar but, in any sample, females in this and the sixth instar occur in approximately equal numbers. The evidence suggests that the females moult with increase in size once after attaining maturity, but the possibility of females becoming mature in either the fifth or the sixth instar is not completely excluded. Only one female having the number of joints of the flagellum of the antenna corresponding to that in the seventh instar of the male has been found, although several hundred females have been examined. It is therefore concluded that if the females moult before each brood, as in the majority of isopods, female *I. viridis* from New England Creek usually do not change their bodily dimensions after the sixth instar. It seems unlikely that females would use the same brood pouch for successive clusters of eggs, especially since moulting is so commonly bound up with the opening of the vagina and hence with fertilization. No females with torn marsupia were ever found although in many the brood pouch was quite empty. Probably the females retire to the depths of the creek to moult. Alternatively, the females may have but one or two broods and then die. The data available do not permit of a decision being made on these points.

The fact that the great majority of the females never grow after reaching the sixth instar, while the males undergo a further moult, explains why the male of a copulating pair is always larger than his mate.

The "Przibram quotient", i.e. the ratio between the length of an animal at a given instar and that at the preceding instar, has been calculated. According to Przibram's (1931) theory, arthropods double in weight from instar to instar and hence, assuming that the body does not alter in form, the corresponding ratio for increase in length should be $\sqrt[3]{2}$, i.e. 1·26. The figures given suggest that this "law of geometrical progression" may be applicable to the growth of *I. viridis*.

CHANGES IN BODILY FORM

The post-embryonic changes in bodily form and in the shape of some of the appendages of *I. viridis* have been investigated. There is considerable change both in the shape and proportions of different parts from instar to instar and, in this paper, only those parts showing the most marked and what are believed to be taxonomically the most significant changes, are dealt with. These changes are described in two ways: (*a*) where no irregular alteration in shape is involved, a series of measurements has been made and plotted on a double logarithmic grid to test for simple allometry (Huxley & Teissier, 1936); (*b*) where changes in shape not easily susceptible to measurement, or in number of joints, etc. do occur, e.g. uropods or antennae, these have been illustrated serially in Figs. 7, 8 and 13 and are described in the text.

Allometry

Measurements were made on 141 unsexed and male *I. viridis* and on 45 females. Females were only distinguished from the fifth instar onwards. The dimensions selected for discussion are illustrated in Fig. 9; actually many more dimensions were measured, but, since the object was primarily to facilitate the description of morphological changes rather than to discuss "relative growth", they have been omitted.

The dimensions taken (Fig. 9) are, the greatest breadth of the cephalon and of the third and sixth thoracic segments, including the coxal plates, the length of the seventh thoracic segment and the length of the abdomen: the first three are compared with the total length as the standard, measured from a line drawn transversely between the tips of the antero-lateral projections of the cephalon to the posterior tip of the abdomen, the fourth with the total length minus the length of the seventh thoracic segment, and the fifth with the length of cephalon plus thorax only. "The law of simple allometry can be expressed by a formula of the type, $y = bx^{\alpha}$, where y is the part, x the standard or whole, and b and α are constants" (Huxley & Teissier 1936, p. 780) so that if simple allometry is acting, the graph of $\log y / \log x$, is a straight line (Huxley, 1932).

In this paper, the three standard dimensions described above are taken as x and the other five as the compared dimension y.

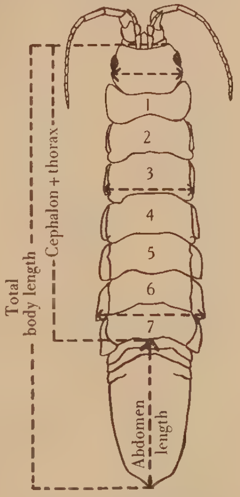


Fig. 9. *Idotea viridis.* Dimensions employed in discussion on allometry.

The best fitting line to the plot of the logarithms of x and y has been calculated from the logarithms of the measurements by the method of least squares. No attempt has been made to group the data since it was difficult to decide upon a suitable basis of classification. Grouping according to size would cause animals from different instars to be placed in the same class and grouping in instars seemed unwise owing to the considerable overlap between adjacent instars (Table I). The values obtained for α, the equilibrium constant or growth constant (Huxley & Teissier, 1936) only are given since the constant b depends on the units of measurement employed and has been altered in the graphs (Figs. 10, 11), to avoid superimposing them. In the animals examined, the body length ranged from 1·6 to 13·4 mm.

The graphs of $\log y / \log x$ (Figs. 10, 11) do appear to fall reasonably well on a straight line and it is therefore concluded that simple allometry is at work and that the "growth constant" α may justifiably be calculated from the data.

Sixth thoracic segment (Fig. 10B).

In adult males the body is at its broadest in the region of the fifth and sixth thoracic segment, which rarely differ significantly in breadth. The "growth constant" of the breadth of this segment, body length being used for comparison, therefore gives valuable information as to whether the animal as a whole becomes slimmer or broader during growth: further it is chosen in

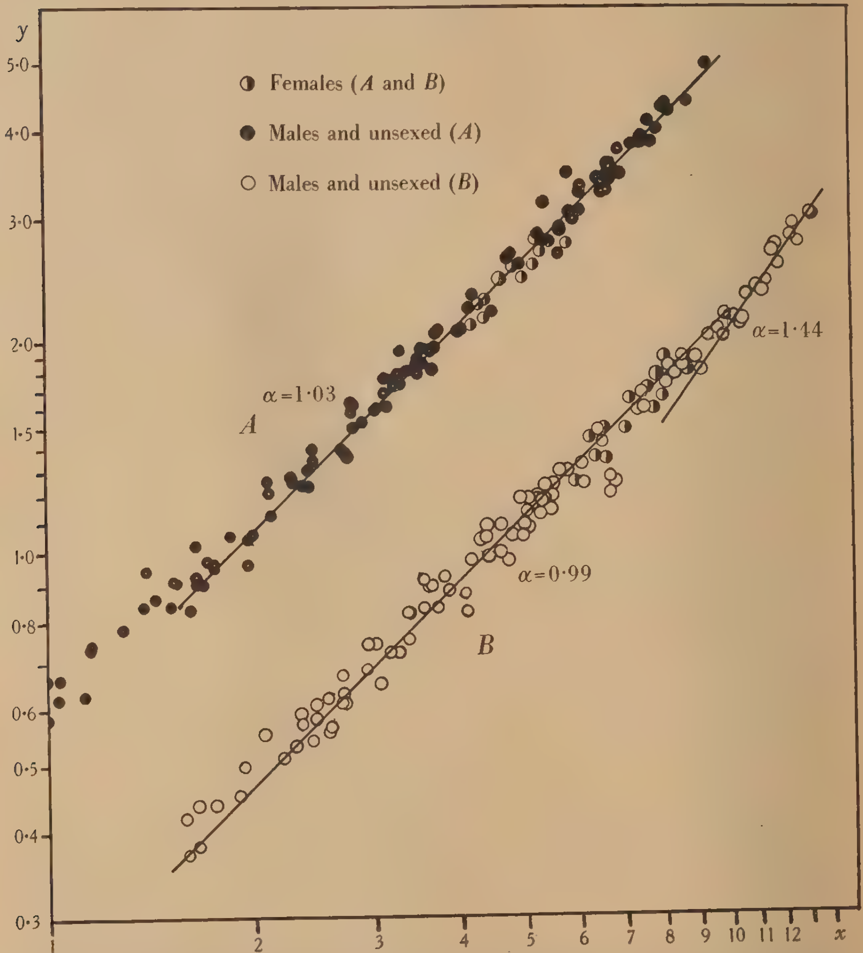


Fig. 10. A (upper line); length in millimetres of abdomen (y) plotted against length of cephalon + thorax (x). B (lower line); breadth in millimetres of 6th thoracic segment (y) plotted against total body length (x). Both double logarithmic plots.

preference to the fifth segment because, in the females, it is less likely to be influenced by the broadening of the more anterior segments concomitant with the formation of a marsupium. It is to be doubted whether the value of α, 0·994, differs significantly from 1, so that up to and including the sixth instar, the sixth thoracic segment in the unsexed animals and in males and females grows isometrically with the body length and the overall bodily dimensions are unaltered. In the seventh instar the body becomes stouter, since the constant is now 1·44. It is interesting that the sixth thoracic segment in the female behaves as that of the male and is uninfluenced by the formation of the brood pouch.

TABLE II. VALUES OF α

x	y	α	Notes
Total body length	Cephalon breadth	0·83	
Total body length	Breadth of 6th thoracic segment	1·44	Instar VII
		0·99	Instars I–VI inclusive
Total body length	Breadth of 3rd thoracic segment	0·88	Males and unsexed
		2·41	Females, instars V? and VI
Total body length minus length of 7th thoracic segment	Length of 7th thoracic segment	2·03	Instar VII
		1·15	Instars III–VI inclusive
		irregular	Instars I and II
Length of cephalon plus thorax	Length of abdomen	1·03	Instars II–VII
			Animals in instar I appear to deviate from line

Third thoracic segment (Fig. 11 A).

The third thoracic segment is the widest in the adult female. The widening appears to take place at the ecdyses between the fourth and fifth, and fifth and sixth instars, and if the line is produced back to meet that for unsexed animals and males, it cuts the latter at a point equivalent to a body length of 6·3 mm. This is fairly close to the mean length (5·9 mm., with a range of from 4·9 to 7·5 mm.) of animals in the fifth instar, and suggests a sudden rather than a gradual response to the developing gonads. The "growth constant" (0·88) of this segment for unsexed animals and for males shows that it becomes proportionately narrower with increasing age, so that the widest region of the thorax moves back to the sixth thoracic segment.

Seventh thoracic segment.

The seventh thoracic segment of the newly hatched animal is very small: at the first moult it doubles in length and then thereafter up to and including the sixth instar has a growth constant of 1·15 compared with the total length minus the seventh thoracic segment. In the seventh instar the constant rises to 2·03.

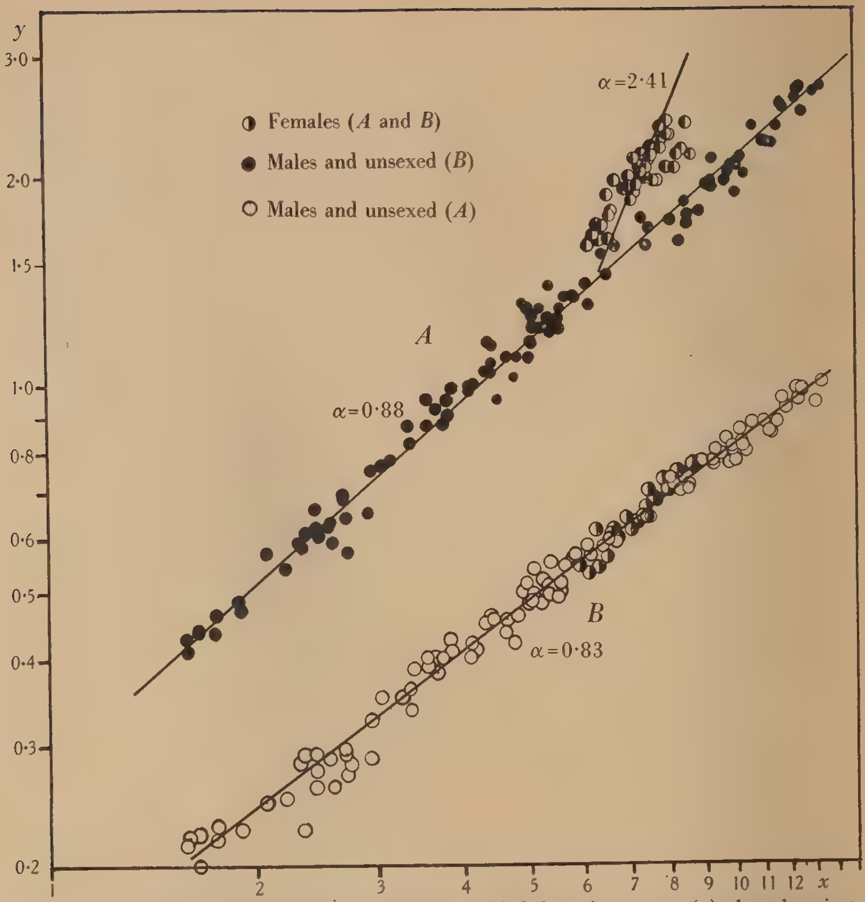


Fig. 11. A (upper line); breadth in millimetres of third thoracic segment (*y*) plotted against total body length (*x*). B (lower line); breadth of cephalon/2 (*y*) plotted against total body length (*x*). Both double logarithmic plots.

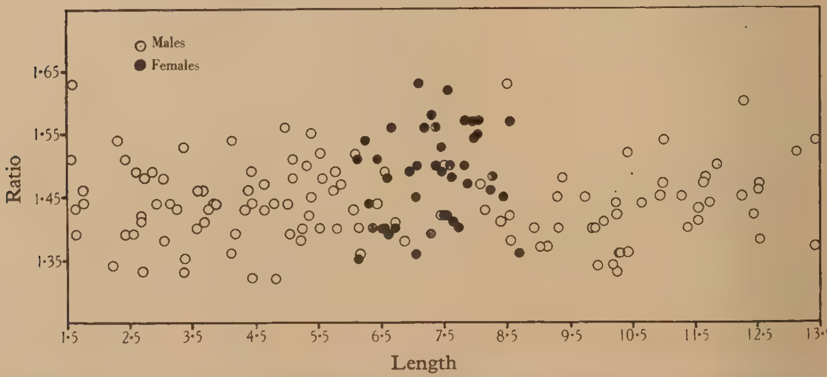


Fig. 12. Ratio cephalon breadth/cephalon length of individual animals plotted against total body length (anterior border of cephalon to posterior tip of animal) in millimetres, showing that the ratio does not change as the animal becomes bigger.

Cephalon (Figs. 11B, 12).

The cephalon becomes proportionately narrower and shorter with age compared with the rest of the body but the ratio length/breadth of its overall dimensions does not change although its anterior margin becomes convex anteriorly and there is some change in outline. The relatively enormous cephalon of the newly hatched *Idotea* is shown in Fig. 7*a*.

Abdomen (Figs. 10A, 13).

The proportion of abdomen to thorax plus cephalon does not change significantly after the second ecdysis. There is some evidence from the graph that in the first two instars the growth constant is less than 1 and while both the number of points and their wide scatter make it difficult to come to any definite conclusion, it is clear that this is correlated with the doubling in length of the seventh thoracic segment during the first post-embryonic moult. Following this, the abdomen grows isometrically with the cephalon plus thorax. Since this is so, and since the growth constant of the cephalon is 0·83, it follows that the thorax (morphologically the second to eighth thoracic segments) occupies an increasing proportion of the total length as the animal becomes older. The ratio breadth/length of the abdomen remains constant at approximately 1·9 throughout the whole post-embryonic period, hence the same growth constant is applicable to its breadth as to its length.

CHANGES IN SHAPE

Seventh thoracic segment (Fig. 7*c*, *d*, *e*, *f*; Table II).

I. viridis is hatched with a small, limbless seventh thoracic segment, as is usual in isopods. In instar II this segment becomes proportionately larger in all dimensions, doubling in length, although the total length of the animal is only 1·44 times as long as in instar I, and short limbs are present. It continues to grow at a rapid rate, increasing in size proportionately to the other segments at each instar until in instar V it is only a very little shorter than the longest thoracic segment. In the last instar it again shows a sudden proportionate increase in length.

Coxal plates (Fig. 7*c*, *c′*, *d*, *d′*, *e*, *e′*, *f*, *f′*).

As has been stated above, *I. viridis* is hatched with exceptionally large coxal plates (Fig. 7*a*, *c*, *c′*) and it is especially noteworthy that not only do they occur on the six posterior thoracic segments but that they are large and conspicuous on the first. In the second instar, the coxal plates of segment one are no longer visible from the dorsal surface but their lateral boundaries can still be seen on the ventral surface (Fig. 7*d′*). It is believed that they are still present in all later instars but fuse with the ventral side of the segment

(Fig. 7*e'*, *f'*, shaded area on first thoracic segment). The lateral expansions of the first thoracic segment would therefore be the pleura of that segment which have not been replaced by the coxal plates (Calman, 1909, p. 202). Clearly it is impossible to follow the behaviour of these coxal plates without histological examination. The coxal plates on thoracic segments two, three and four of animals of instar I are comparatively large; in the second instar they have increased proportionately in size and have become very convex laterally, but do not occupy the whole of the lateral margin of the segment (Fig. 7*d*). The pleura are small (Fig. 7*d'*). In instar III (Fig. 7*e*, *e'*) the coxal plates have become flattened and have diminished in size relative to their segments and the pleura have grown out laterally behind them. In instar IV (Fig. 7*f*, *f'*) the coxal plates have become more flattened, have extended to the anterior border of the segment, and the pleura are now flush with their outer borders. This is the adult condition and no further changes of any magnitude occur. The whole process can be summarized as initial growth of the coxal plates followed by a change in shape accompanied or possibly induced by later growth of the pleura. On segments five, six and seven the same process occurs except that there is no late growth of the pleura.

Antennule.

The changes in shape of the antennule of the successive instars are illustrated in Fig. 13*a*, I–VII. Apart from the gradual assumption of the adult form, the most obvious changes are in the flagellum. In instars I and II this latter is conical and bears only one aesthetasc. In instars III, IV, V and VI it becomes first of all cylindrical and then rounded at its antero-medial border; at the same time the number of aesthetascs increases from 2 to 3, 3 to 4 and 4 to 6 respectively. In the last instar the antero-medial margin becomes sloped and there are eight aesthetascs arranged in a series along the slope. The change in shape of the flagellum along its antero-medial border appears to be due largely to the increase in the number of aesthetascs. Round the base of each of these the exoskeleton appears to become flattened and hence when they cease to be confined to the tip of the flagellum and spread along its antero-medial margin, this becomes terraced.

Antenna (Fig. 8).

The changes in the number of joints of the flagellum of the antenna have already been discussed. The peduncle chiefly shows a thickening of the joints.

In the female, both antennule and antenna have the form characteristic of the sixth instar.

Maxillula.

The first maxilla possesses its characteristic number of spines from the first instar onwards but at first they may be smooth and they may not achieve the toothed condition characteristic of the adult until the fifth or sixth instar. This is variable.

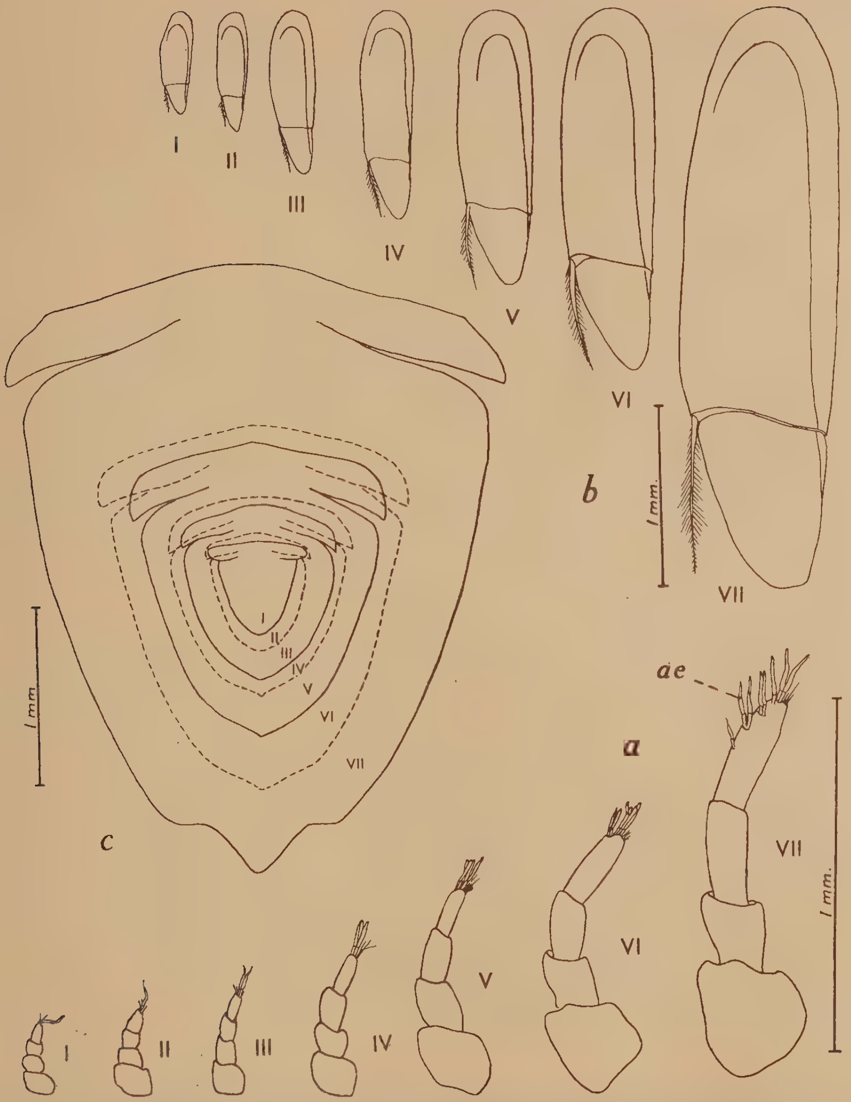


Fig. 13. *a*, antennule of different instars of *Idotea viridis* showing change in shape of flagellum and increase in number of aesthetascs (*ae*); *b*, right uropod from anatomical ventral surface (in these two cases the appendage of the newly hatched animal is on the left and the number below each appendage refers to the instar to which the animal belongs); *c*, abdomina of different instars, numbers indicating the instar, newly hatched animal in centre. The boundaries of the abdomina of alternate instars are dotted for clarity. The preparations were made by dissecting out pleopods and soft tissues and pressing abdomen flat.

Abdomen (Fig. 13*c*, I–VII).

The shape of the posterior part of the abdomen varies from instar to instar, as shown in the figure. The posterior tooth appears first in the fourth instar, the postero-lateral angles in the sixth instar and only in the seventh is the characteristic adult form assumed. The shape of the exoskeleton of the female abdomen is characteristically that of the sixth instar but the arrangement of pigment and of melanophores is usually such as to emphasize the postero-lateral angles.

Uropods.

Since these fold over on the ventral surface of the abdomen, forming the floor of a box enclosing the pleopods, it is to be expected that their changes in shape are correlated with those of the posterior fused segments of the abdomen. This is indeed the case (Fig. 13*b*, I–VII). The flattened posterior border of the uropods in instar VII is correlated with the fact that with the full development of the posterior tooth and lateral angles of the abdomen, the uropods do not form a floor on the ventral surface of the tooth, but run straight across from the transverse straight portion of the postero-lateral angles.

DISCUSSION

The data on the biology of *Idotea viridis* from New England Creek have been briefly discussed above and since they are not necessarily applicable to *I. viridis* from other habitats or to the genus in general, will not be further dealt with.

Relative growth in an isopod, *Asellus aquaticus*, has recently been investigated in detail by Needham (1937) and it is of interest to see how far his results aid in the interpretation of the less extensive data obtained with *Idotea viridis* and how far the relative growth of the two animals is similar. The data given here are for post-embryonic development only and would therefore fall during Needham's "later period of simple allometry" but it seems possible that persistent rhythmic variations in α occur in *I. viridis* as also in this period in *Asellus aquaticus* (Figs. 10, 11). The values of α in *Idotea viridis* compared with those obtained by Needham (Table II, p. 293) in *Asellus aquaticus* are as follows:

		I. viridis	*A. aquaticus* (Needham, 1937)
Cephalon breadth	Males and females	0·83	0·80
3rd thoracic segment breadth	Males and unsexed	0·88	1·06
	Females, instars V? and VI	2·41	1·15
6th thoracic segment breadth	Males, instars I–VI inclusive	0·99	1·06
	Instar VII	1·44	
	Females, instars I–VI	as for males	1·01
Abdomen width		1·00 (approx.)	1·00

On the whole there appears to be a general similarity in the results obtained with the two animals. The cephalon (head plus morphological 1st thoracic segment) breadth is negatively allometric in both species and the values of the growth constant surprisingly close. On the other hand, *Idotea viridis* becomes slightly slimmer or retains nearly a constant build up to and including the sixth instar, while *Asellus aquaticus* becomes slightly stouter.

There is considerable evidence that the changes in regional growth rates follow the same plan in both animals. The broadest region moves back in *Idotea viridis*, as in *Asellus aquaticus*, and similarly the sixth thoracic segment becomes the broadest in adult males, while in the females the broadest region moves forward at maturity to the third thoracic segment. Needham's (1937, p. 306) discussion on the question of the occurrence of a "metamorphic moult" has important bearings on the suddenness of the change in growth rate of the third thoracic segment in the female *Idotea viridis*. It does appear that in *I. viridis* there is in fact a "metamorphic moult", between the fourth and fifth instars, but the number of points above the line between total body lengths of 5 and 6 mm. (Fig. 11 A) suggest that the growth centre may neither move forward so rapidly as the diagram suggests, nor may the growth constant for the third thoracic segment be so high. This appears to be in agreement with the findings of Needham, but, since this worker does not claim that his groups correspond to instars, it is difficult to find an exact parallel in the two cases. There seems to be no sign of a corresponding sudden widening of the third thoracic segment in the male *I. viridis*, although there is in *Asellus aquaticus*, and Needham's fig. 4 gives no evidence of the sudden widening of the sixth thoracic segment in the male *A. aquaticus* such as occurs in *Idotea viridis*. Sudden changes in bodily form as the gonads mature appear to be characteristic of *I. viridis*.

As in *Asellus aquaticus* (Needham, 1937, p. 310), the difference in shape of the sexually mature *Idotea viridis* is correlated with their breeding habits. The brood pouch is developed in the region of the anterior thoracic segments, hence their wideness, and similarly the relative breadth of the fifth and sixth thoracic segments in the male is probably correlated with his carrying the female underneath his body while mating.

The data on relative growth show that the form of *I. viridis* does change from instar to instar and it is therefore not to be expected that if the volume is doubled at each moult the "Przibram quotient" will equal 1·26 in every case. Table I shows that in the earliest moults when the seventh thoracic segment is increasing rapidly, the quotient exceeds 1·26, in other words the animal lengthens in proportion to its volume; for the moults between the third and fourth, fourth and fifth, and fifth and sixth instars when other data show that there is little change in form, the quotient is very close to 1·26; while when the seventh thoracic segment again suddenly increases in length (Table II) between the sixth and seventh instar of the males, the quotient again rises. The values given in Table I, taken in conjunction with the other data, strongly suggest that the "law of geometrical progression" is applicable to the growth of *I. viridis*. There appear to be no similar data available for other isopods with which these results can be compared.

The changes which, while not easily lending themselves to measurement, are presumably caused by differential growth rates similar to those discussed above, are striking, especially those of the coxal plates (Fig. 7*c*–*f*′). *I. viridis* is hatched with large coxal plates on all the thoracic segments, except the maxillipedal, including the anatomical first, on which they are large and conspicuous. The coxal plate on the first thoracic segment later becomes indistinguishably fused with the pleuron in the adult. As growth proceeds, the relative size of the coxal plates is reduced, partly maybe owing to the proportionate increase of soft parts relative to exoskeleton setting up mechanical stresses which tend to pull them below the pleura, but also, at any rate in segments two, three and four, by the late growth of the pleura. Since in the Asellota the coxopodite is still movably articulated with the body (Calman, 1909), it might be expected that the fusion of the coxopodite with the body, and hence the formation of coxal plates, took place late in the phylogeny of the Isopoda and that the coxal plates would appear late in ontogeny. If so, apparently the evolutionary process has become reversed and, while originally lateral growth of the pleura preceded growth of the coxopodite, it now takes place the other way round.

The increase in the number of joints in either the antennule or the antenna during growth is probably of widespread occurrence in Crustacea where one of these appendages is very long. Schellenberg (1938) has recorded an increase in the number of joints of the outer flagellum of the antennule of *Niphargus tatrensis* var. *aggtelekiensis* similar to that found in the antenna of *Idotea viridis*. The changes in the antennule and maxillula are of the type that might be expected to occur during growth and are regular throughout. On the other hand, the abdomen and hence the uropods assume their final characters somewhat suddenly. Bate & Westwood (1868, vol. II, p. 381) observed the "comparative paucity of the articulations of the lower antennae in young individuals" of *I. tricuspidata* (now *I. baltica* (Pallas)) and that animals from the British Museum collection exhibited "variations in the form of the terminal segment of the body, with the length and size of the respective specimens". Again, Tattersall (1906, p. 48) in discussing *I. baltica* states that "Young examples of this species are difficult to distinguish from such species as *I. pelagica*, *I. granulosa* and *I. viridis*, in which the telson has a very similar shape". On the other hand, Collinge (1917, p. 728) states that he found very few variations in the form of the antennae, apart from the number of joints in the flagellum, or in the shape of the terminal segment of the body, and Sars (1899, p. 81) found the terminal segment in *I. baltica* "to be pretty constant even in very young specimens". No data on the development of an idoteid other than those given in this paper appear to be available, but, on the grounds that positive evidence outweighs negative evidence, there is reason to believe that changes in shape of the abdomen occur during growth in *I. baltica* as they do in *I. viridis*, to which species the observations of Bate & Westwood are decidedly applicable since the shape of the abdomen changes considerably during growth (Fig. 13). How far these observations can be further extended to other species remains to be seen.

Huxley lays great stress on the important bearing of allometry on taxonomy and states (1932, p. 204) "systematists are agreed that mere size differences may have no taxonomic significance...but they usually attach much greater importance to differences in the *percentage* size of parts. Our studies of heterogony (i.e. allometry), however, make it obvious that such differences may have precisely as little taxonomic significance as those in absolute size." If one includes under allometry all the changes observed during the post-embryonic development of *I. viridis*, the relevance of Huxley's remarks is at once apparent. Collinge (1917, p. 737) uses body shape, width of coxal plates and shape of abdomen in his key to the British species of the genus *Idotea* and in this paper it has been suggested that the first and the last of these be employed as diagnostic characters of *I. viridis*: it has, however, been shown above that not one of these characters is constant throughout the whole post-embryonic life of *I. viridis* and, since little is known of the early instars of closely related forms, it may prove difficult to distinguish between them. Further, additional characters such as the shape of, and number of aesthetascs on, the flagellum of the antennule vary from instar to instar, as do the number of joints in the flagellum of the antenna. Only the ratio breadth/length of the cephalon and the number of spines on the outer lobe of the maxillula emerge as constant throughout the whole period.

It is quite easy to see that if males and females of *I. viridis* became sexually mature either one instar earlier or later than they do in New England Creek, they would differ from the New England Creek adults in general appearance or "habitus", in the proportions of many parts and in the shape of the abdomen. There is evidence that a process of this nature does occur. Adult males of *I. viridis* from different localities may vary in body length from 9 to 23 mm., although 12 mm. appears to be the commonest length (Collinge, 1917, p. 729).

The change in shape of the abdomen has been investigated in specimens from Mr Spooner's and my collections (Fig. 14); the results show that in small adult males, while the postero-lateral angles of the abdomen do appear to be considerably less marked than in larger forms, the median tooth is much less affected, although in the smaller forms (*a* and *b*) there is some tendency for the abdomen to be similar in shape to that of the fourth and fifth instars of the New England Creek form. It has proved to be possible to arrange the abdomens in series according to the development of the postero-lateral angles and a comparison between Figs. 13 and 14 shows that this follows fairly closely the ontogenetic sequence. The correlation between size and shape is not very clearly marked but close correlation is not to be expected

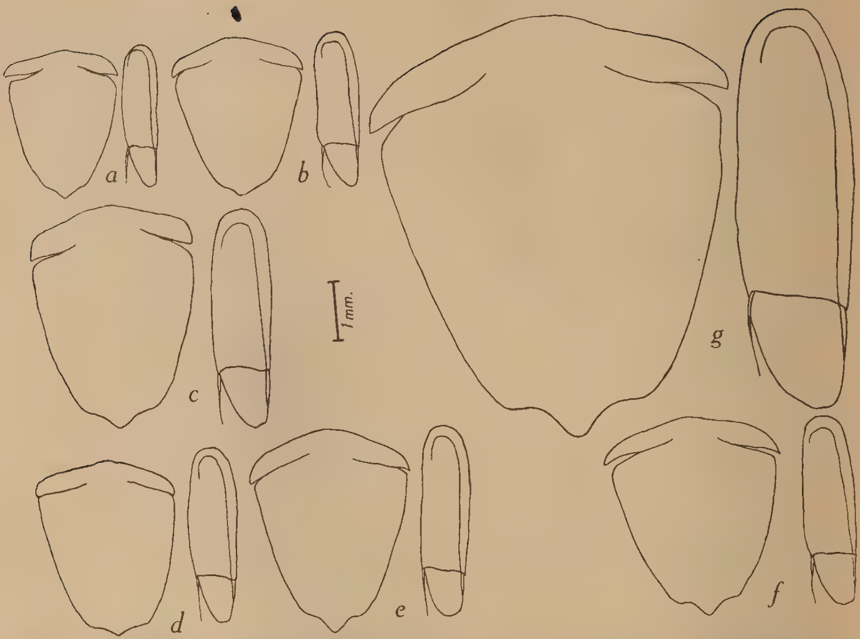


Fig. 14. Abdomens of adult male *Idotea viridis* from various localities arranged in series to illustrate the different degrees of development of the postero-lateral angles. Right uropods showing correlated changes in shape are included. The abdomens have been prepared by flattening after removal of pleopods and tissues. In the following table, when animals from two localities are entered under the same letter, the first only has been drawn, since the abdomens from males from both sources are similar.

Abdomen and uropod.	Source	Length of mature ♂ mm.	Collected by
a	Wivelscombe, High Marsh, Tamar	9·0	G. I. Crawford
b	Ernesettle Flat, Tamar	9·5	G. M. Spooner
	Langton Herring, Fleet	11·0	,,
c	Zostera pools, Maplin Sands, Essex	12·0	N. H. Howes
	Brackish pool inside sea wall, Holbeach, the Wash	14·6	G.M.S.
d	Lodmoor, Weymouth	10·0	,,
e	Thorn Point Causeway, Tamar	11·4	,,
f	New England Creek, Gt Wakering, Essex	12·0	N.H.H.
g	Brackish pool inside sea wall, near Cupid's Corner, Gt Wakering, Essex	22·2	,,

The localities in the Tamar Estuary mentioned above will be found in a map given by Hartley & Spooner (1938).

since comparatively few specimens were available and the range of size in each instar is considerable (Table I). It must be concluded that although the attainment of sexual maturity at a small size, or at an earlier instar than usual, i.e. paedogenesis, causes considerable difference in abdomen shape, other factors, possibly those effecting the precocious onset of sexual maturity, have also some influence on bodily form, for instance, by inducing the early appearance of the median tooth without altering the time of appearance of the postero-lateral angles.

I have pleasure in acknowledging my indebtedness to Prof. H. G. Jackson for much advice, to Mr G. M. Spooner for suggestions and for the loan of much material, to Prof. D. M. S. Watson, F.R.S. for his interest and encouragement and to Mr F. J. Aumonier for technical assistance in the examination of the aesthetascs. The collecting apparatus used in this work was obtained through a grant from the Government Grants Committee of the Royal Society.

SUMMARY

A local race of *Idotea viridis* from south-east Essex is described and its classification as *I. viridis* discussed. This animal is a nektonic form and so far has only been found in New England Creek in south-east Essex. The biology and post-embryonic development of this race is described. Quantitative samples were taken of the animals present in the creek in 1934, 1935 and 1936. *I. viridis* was rare in the first five months of the year; numbers rose to a maximum in late June and July and remained comparatively high until the end of October.

The number of young in the brood pouch is very variable. There is some evidence that the number of fertilized eggs was reduced by the expulsion of embryos before their development was complete. The newly hatched *I. viridis* is described.

There are six ecdyses between hatching and maturity in the males and four or five in the females. The "Przibram quotient" has been calculated between successive instars and there is evidence that the "law of geometrical progression" may be applicable to growth in *I. viridis*.

Changes in external form during post-embryonic development have been investigated by studying the allometry. Changes in shape not susceptible to measurement are also described. The shape of, and number of aesthetascs on, the flagellum of the antennule change from instar to instar. The number of joints on the flagellum of the antenna also increases progressively. The shape of the abdomen changes and the adult form is only achieved in the last instar of the males. The number of spines on the outer lobe of the maxillula and the ratio breadth/length of the cephalon remain constant throughout the whole post-embryonic development.

The taxonomic significance of the changes in shape and in proportions is discussed with reference to collections of *I. viridis* made in other parts of England.

REFERENCES

BATE, C. S. & WESTWOOD, J. O., 1868. *A History of the British Sessile-eyed Crustacea*, Vol. II. London.

CALMAN, W. T., 1909. Lankester's *A Treatise on Zoology*, Part VII, Crustacea. London.

COLLINGE, W. E., 1917. A revision of the British Idoteidae. *Trans. Roy. Soc. Edinb.*, Vol. LI, pp. 721–60.

—— 1918. Oral appendages of marine Isopoda. *Journ. Linn. Soc.*, Vol. 34, pp. 65–93.

HANSEN, H. J., 1925. *Studies on the Arthropoda*, Vol. II. Copenhagen.

HARTLEY, P. H. T. & SPOONER, G. M., 1938. The ecology of the Tamar Estuary. I. Introduction. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 501–8.

HOWES, N. H., 1939. The ecology of a saline lagoon in South-east Essex. *Journ. Linn. Soc.*, Vol. XL, pp. 383–445.

HUXLEY, J. S., 1932. *Problems of Relative Growth.* London.

HUXLEY, J. S. & TEISSIER, G., 1936. Terminology of relative growth. *Nature*, Vol. 137, p. 780.

JACKSON, H. G., 1926. The morphology of the isopod head. Part I. *Proc. Zool. Soc. Lond.*, pp. 885–911.

JANCKE, O., 1924. Die Brutpflege einiger Malakostraken. *Zool. Anz.*, Bd. LVIII, pp. 273–8.

NEEDHAM, A. E., 1937. Relative Growth in *Asellus aquaticus*. *Proc. Zool. Soc. Lond.* A, pp. 289–313.

PRZIBRAM, H., 1931. *Connecting Laws in Animal Morphology.* University of London Press.

SARS, G. O., 1899. *An Account of the Crustacea of Norway*, Vol. II, Isopoda. Bergen.

SCHELLENBERG, A., 1938. Alters-, Geschlechts- und Individualunterschiede des Amphipoden *Niphargus tatrensis*. *Zool. Jahrb.*, Abt. I (Systematik), Bd. 71, pp. 191–202.

SCOURFIELD, D. J., 1896. Olfactory Setae of Cladocera. *Journ. Quekett Micr. Club*, *Ser.* 2, Vol. 6, pp. 280–8.

—— 1905. Die sogenannten "Riechstäbchen" bei den Cladoceren. *ForschBer. Biol. Sta. Plön*, Bd. 12, pp. 340–53.

TATTERSALL, W. M., 1906. Isopoda. The Marine Fauna of the Coast of Ireland. V. *Rep. Sea Inl. Fish. Ireland for* 1904, Part II, Appendix No. II.

ZIMMER, C., 1927. Isopoda, in Kükenthal, W. & Krumbach, T., *Handbuch der Zoologie* Bd. 3. Berlin.

NOTES ON THE BIONOMICS OF THE TUBE-BUILDING AMPHIPOD, *LEPTOCHEIRUS PILOSUS* ZADDACH

By C. B. Goodhart

Gonville and Caius College, Cambridge

(Text-figs. 1–3)

CONTENTS

	PAGE
Introduction	311
The cement glands	312
Construction of the tube	313
Position in the tube	317
Feeding habits	318
Breeding habits and life history	321
Conclusion	322
Summary	323
References	324

INTRODUCTION

It is well known that amphipods belonging to several different families live habitually in nests or burrows built for this purpose. These tubicolous species are all more or less adapted for the construction of tubes, while many have other modifications associated with their feeding habits, which are necessarily rather different from those of the more numerous free swimming species. An inquiry into the natural history of the small brackish water amphipod, *Leptocheirus pilosus* Zaddach, disclosed habits that appear somewhat different from those of the other tubicolous species which have been investigated.

L. pilosus has been recorded from brackish or almost fresh water on most of the coasts of Europe, from the Baltic to the Mediterranean. In England the records are sparse, but the species seems fairly widespread, and probably occurs in most of the estuaries of the British Isles. The whole of the material used in this work was obtained from a sluice pond at Keyhaven near Lymington in Hampshire, which, in September, contained about one-quarter sea water, but which is probably subject to considerable variations. The animal was abundant here, together with the other characteristic brackish water amphipods, *Corophium insidiosum* Crawford and *Gammarus zaddachi* Sexton. It can be kept in the laboratory without much difficulty in shallow dishes containing the alga *Chondrus crispus*, among which it lives, together with a quantity of the detritus from the bottom of the pond. The water in these dishes should not be more than 2 or 3 in. in depth, and overcrowding must be avoided, as the amphipod will only live in well oxygenated water.

Leptocheirus belongs to the family Photidae, the majority of which are known to be tubicolous. It is rather smaller than most of the Amphipoda, rarely exceeding 4 mm. in length, while the characteristic lateral compression of the body has, to a considerable extent, been lost. In a fully grown male the distance between the lower edges of the coxal plates of each side of the body is equal to about a third of the length from head to telson.

When alive the animal is a dark reddish brown on top, while ventrally it is much paler. This colour is due to the presence of a number of large much-branched pigment cells, dark red in colour, situated on the back, the mesosome, and the upper part of the coxal plates. They are fewer on the metasome and urosome, and entirely absent from the appendages, with the exception of the posterior margin of the basal (1st) joints of the last three pairs of peraeopods. These pigment spots are of the type observed by Holmes (1901) in *Amphithöe longimana* Smith, except that the large pale green cells found in this animal are not present in *Leptocheirus pilosus*. Besides the pigment cells the animal is coloured by the gut, which is usually black and opaque; by the gonads, especially prominent in the female, which are yellow or orange in colour; by the eggs, which are dark brown while being carried in the brood pouch; and, in most, by an opaque white patch, which appears to be in the chitin, extending from behind the head to the third or fourth segment of the mesosome. The eye is black.

There is a certain amount of variation in colour among individuals, and they appear to possess the power of altering their colour slightly, but to an even smaller extent than does *Amphithöe longimana*. Several animals were kept in a dish containing part of the thallus of *Ulva* in clear water. After three days the pigment cells were still expanded, although since the gut was empty, the animals were rather paler than at the beginning of the experiment. On the fourth day they all died, probably from lack of suitable food. After death, and particularly in specimens preserved in alcohol, the colour fades considerably, though the pigment cells appear to remain uncontracted. When out of water the body, and especially the coxal plates, has a red and green iridescence. The chitin of the exoskeleton is hydrofuge, and an animal which has become caught in the surface film is unable to break it. This is perhaps due to the mucus secreted from the dermal glands on the coxal plates.

Morphologically the whole genus has been described in detail by Sexton (1911).

The Cement Glands

The presence of glandular tissue in the first and second pairs of peraeopods* of many amphipods was first recognized by Smith (1874), who suggested that they secreted the cement used in tube building. He also noticed that they communicated to the exterior through a pore at or near the tip of the claw. Calman (1909) states that dermal glands are found in the Ampeliscidae on most of the appendages, and in the Talitridae scattered all over the body. Claus (1879) found unicellular glands scattered all over the body of *Phronima*. Holmes (1901) and Skutch (1926) both describe glands in the first and second peraeopods of two tubicolous species of *Amphithöe*, and have observed a silken thread emerging from a pore in the tip of the claw. Neither of them describe any dermal glands in other parts of the body.

---

* In this paper the nomenclature of Stebbing (1906) is followed, and the first pair of peraeopods is accordingly that immediately posterior to the gnathopods, and attached to the third free segment of the body.

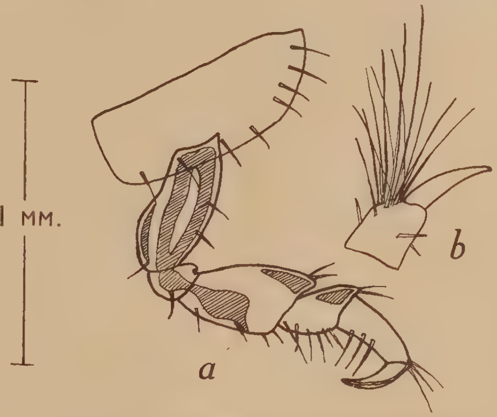


Fig. 1. *a*, Second peraeopod of *Leptocheirus pilosus*; glandular tissue shaded. *b*, Distal end of palmar joint, and claw, of peraeopod seven.

The glands in the peraeopods of *Leptocheirus pilosus* are shown very well when stained in haematoxylin, and cleared (Fig. 1*a*). The two main glands are in the basal (1st) joint, running its whole length, one on each side of the muscle. There is also a smaller one behind these two. They join together distally and pass through the ischial (2nd) joint, where they are slightly expanded, into the meral (3rd) joint in whose proximal end they are again expanded. Besides these there are two smaller pieces of glandular tissue in the distally dilated ends of the meral (3rd) and carpal (4th) joints. All these glands connect (probably by some sort of a duct, though none can be seen) with the canal which runs along the upper edge of the claw, to open at a pore in its truncated tip.

Besides these glands in the first and second pairs of peraeopods, dermal glands are found scattered over the body, being especially numerous on the coxal plates. These glands probably secrete a mucus cement in the same way as do the similar glands in the Talitridae.

The Construction of the Tube

Three different types of amphipod tube have been described, and that of *Leptocheirus pilosus* belongs to a fourth.

The first type is the Sand Burrow, and the least specialized sand burrows are built by members of the family Talitridae. These have dermal mucus glands scattered all over their bodies and as the animal burrows, the sand grains lining the burrow are probably smeared by this mucus, and hence stick together, preventing the walls of the burrow from caving in. Reid (1938) has described the digging habits of *Talorchestia deshayesii* (Audouin), and in this species at any rate the burrow is not permanent, but is filled up immediately behind the animal. Hence the mucus secreted on to the sides of the burrow can never harden into a permanent cemented wall.

Hunt (1925) gives a brief account of the tube of *Ampelisca*, which is of rather a more permanent nature. The animal burrows into the sand, and curls up just below the surface, with the head and antennae projecting out of the entrance. A cement is secreted from the dermal glands, which are on all the legs, and this becomes mixed with the grains on the inside of the burrow, eventually hardening into a purse-like tube in which the animal lives. No form of silk is produced and indeed it would scarcely be possible for the sand grains to be bound up by a silken thread. A similar type of semi-permanent sand burrow has been described in *Microprotopus maculatus* Norman by Schellenberg (1929). These tubes are still burrows, being supported on all sides by the surrounding sand.

The second type is the Mud Burrow, as described by Hart (1930) in *Corophium volutator* Pallas. The wall of the U-shaped burrow is strengthened and prevented from falling in by a secretion of mucus from the glands, which is mixed with the mud as the animal burrows through it. This ultimately hardens. Here again no silken thread was observed. This burrow is semi-permanent and is kept open while it is inhabited. Hart also notes that under some circumstances *Corophium volutator* can build a clumsy and fragile tube of mud and algal fragments, instead of the more usual burrow below the surface of the mud. In *C. insidiosum* I have noticed that a similar tube is the one normally used. This species does not appear to burrow.

The third type is a true tube built of comparatively large pieces of material, dead vegetation, living algal filaments and small stones, all bound together by strands of the so-called "amphipod silk". This type of nest was found in two species of *Amphithöe* by Holmes (1901) and Skutch (1926), and is probably the most highly specialized. The only cement glands are those in the first and second pairs of peraeopods, and from the pores in the claws of these legs is spun a definite silken thread, which is fixed to the nest-building materials while still adhesive, later hardening. The finished nest consists of a bundle of algal filaments, etc., bound together by silk, down the middle of which runs the cylindrical tube lined by a silken web.

The tube of *Leptocheirus pilosus* belongs to a fourth type, and, as far as specialization is concerned, lies between those of *Corophium* and *Amphithöe*. *Leptocheirus pilosus* belongs to a family which is probably related to the Amphithoidae, though its members are in general not so specialized for a tubicolous existence.

This tube is a flat blister-like capsule fixed to the smooth surface of the thallus of *Chondrus crispus*, or to the upper sides of smooth stones. If the animal is kept in a glass vessel it will build its tube against the glass. The capsule is slightly longer than the animal which lives in it and rather more than half as broad as long. It is open at both ends, and the area of the mouth is considerably less than that of a cross-section through the tube in the middle, leaving an exit just large enough to allow the animal to get out. The wall of the tube is built of microscopic particles of detritus, mud and sometimes a very few short lengths of red or green algal filaments seldom more than five cells long. These are all cemented together into a relatively tough, thin and flexible wall fixed to the surface by its edges. The inner wall of the tube is formed by the bare surface against which it is built, and there is no lining of mud on this side. Thus if the tube is built against a piece of glass, the animal in the tube can be observed under natural conditions through the glass, which would not be possible with any of the other amphipods which have been examined. There is no question of a tube of long algal filaments bound together by "amphipod silk", as is found in *Amphithöe.*

When *Leptocheirus pilosus* is put into a vessel containing some of the detritus from the bottom of its pond, it will swim about for five minutes or so immediately above the bottom, trailing its last three pairs of peraeopods in the mud. Detritus becomes entangled in the long hairs on the distal ends of the palmar (5th) joints of these limbs (Fig. 1 *b*), and is probably mixed with mucus, which covers the body. It is not, however, secreted from any pore in the claws of these posterior peraeopods. Soon the animal has a short trail of particles, perhaps a millimetre long, attached to these setae. It then settles down, usually in an angle of the dish where the mud lies thickest, and clears a patch for itself by the powerful beating of the pleopods. Next it lies on its side and begins to build the tube, starting with the trails of mud that have been collected on the posterior peraeopods. These are manipulated by the two anterior pairs of peraeopods and also by the gnathopods, and are fixed to the glass by a mucus cement secreted from the pore at the tip of the claw. No silken thread can be seen emerging from this pore, as in *Amphithöe.*

While building the nest the animal frequently turns through 180° to face the other way and goes on building on the other side, until soon it lies within a belt of mud particles cemented loosely together, and fixed above and below its body to the glass. Meanwhile the pleopods are beating strongly in metachronal rhythm, creating a steady current. The flow is from head to telson below the body of the animal, down the space enclosed on either side by the deep coxal plates which are further apart than in most amphipods.

Any particles of suspended detritus near the head of the animal are drawn in under its body and caught in the sieve setae on the second gnathopod, in the same way as is the food, as described further on. These particles are combed off by the claw and palmar joint of the same gnathopod and are worked into the incipient tube by the first and second peraeopods. The animal is continually somersaulting round to face in the opposite direction, and the particles caught are thus packed on to the tube at each end alternately. This packing is done by the first and second pairs of peraeopods which are especially adapted for the secretion of cement from their hollow claws. Since the particles are worked by these claws, they will be well covered with cement which later hardens, sticking them together.

Under natural conditions the water in the pond is not still, either flowing out rapidly through the sluice, or on the flood tide, coming into the pond from the river at the other end, or leaking back through the faulty sluice gates. It therefore carries a considerable amount of suspended matter which would normally soon sink to the bottom, and hence there is an adequate supply of suitable building material in the water flowing over the *Chondrus* plants which grow, several inches above the bottom, on the stone walls leading up to the sluice gates. It is here that *Leptocheirus pilosus* lives and builds its nests. It will not live in foul black mud and does not build its nest on the undersides of stones lying in the mud, neither does it burrow.

The time required to complete the tube depends on the amount of building material available. With an adequate supply it is usually finished in about half an hour.

A newly made tube is comparatively loose and fragile, especially on the outside, where the particles of detritus are not firmly cemented together. More suspended particles are continually sieved out of the respiratory stream by the setae on the second pair of gnathopods, and these, together with the faeces, are worked into the wall from the inside by the anterior peraeopods. More cement is all the time being secreted on to the lining of the tube, both from the peraeopods, and from the dermal glands in the coxal plates which are in contact with different parts of the tube whenever the animal changes its position. The loose outer layer is soon washed away by the stream which, at some states of the tide, flows rapidly over it. Thus the finished tube, which may take a day or two to build, consists of the lining of the original one, composed of small particles of mud, tightly packed and cemented together into a tough and flexible wall well able to withstand the ebb tide which may flow over it with considerable force. It is not called upon to survive wave action.

This tube may be compared to the lining of the burrow of *Ampelisca* or *Corophium*, which is above the surface of, and not supported by the surrounding mud or sand. It is stronger than the lining of a burrow, though still composed of mud particles packed and cemented together by the dermal glands. No silken web is developed and for this reason the tube is more primitive than that of *Amphithöe*.

A series of experiments was conducted to find what use was made of different building materials. Four types were investigated.

(1) Natural detritus. The tubes were built in under half an hour.

(2) Detritus dried by combustion. As above.

(3) *Ulva* thalli. Where a large piece was provided the animals would, after several hours, come to rest in the wrinkles on the surface. Where there were many small shreds of one square millimetre or so, they would be collected together in a corner of the dish, the animal lying underneath the

pile. After a day or more some of the pieces are very loosely bound together in a thin mucus film.

(4) Silver sand. The specimens, after several hours, settle down on the sand and loosely cover themselves with grains. After a day the sand grains cohere very loosely, and if the "tube" is detached from the glass it can be towed about in the water by a pair of forceps without coming to pieces. It will not support its own weight out of the water. When examined under the microscope the sand grains are seen to be held together on a net of very fine, irregular and anastomosing threads. These are probably secreted from the claw ducts on the 1st and 2nd peraeopods alone, and the fragility of the structure is due to the fact that the grains are too large to be cemented together by the secretions from the coxal plates.

If the first and second pairs of peraeopods are removed from an animal it will live for several days, but is unable to build a tube. The glands on these legs are therefore essential for the building of the tube, and the first loose covering is probably cemented by mucus from these alone. Only at a later stage, in the formation of the tough permanent wall, are all the cement glands used to bind all the particles firmly together. As a control, some specimens were observed, from which the fourth and fifth pairs of peraeopods, which carry no cement glands, had been removed. These were able to construct normal tubes, and it follows that the shock of removing four legs would not be sufficient to account for the inability of the specimens in the previous experiment to build their tubes.

Position in the Tube

If the bottom of a glass dish is covered with microscope cover-slips, and the dish is then filled with muddy water and a number of *Leptocheirus pilosus*, the animals will soon have built their nests on the cover-slips which may then be turned over, the four corners being supported with plasticine. The animal can now be observed in its tube under conditions which are much more natural than would be possible with most other tubicolous amphipods, which surround themselves with complete cylindrical walls of opaque materials.

L. pilosus lies with its head just inside the mouth of the tube, with the antennules waving about in the water outside. The antennae are generally held motionless, and pointing downwards. In the female the meral and carpal joints of the first gnathopod are horizontal, and at right angles to the first two joints. The gnathopods are small, and are not crossed. They are in constant movement and help to convey food to the maxillipeds and thence to the mouth. Even when there is no food, the claw is continually opening and shutting. The first gnathopods of the male, which are very long, are tightly crossed under the head (Fig. 3). The palm often projects just out of the mouth of the tube while the limb is practically still. The claw and palm are too far from the mouth to be of any assistance in feeding. They are indeed a hindrance to the animal when changing its position in the tube, and I know of no other genus of Amphipoda which carry their gnathopods in this way. No suggestion is put forward to explain the reason, if any, for this position. In other respects the position in the tube is the same for both sexes (Fig. 2). The body is arched, the mesosome being above the head, while the urosome is held vertically downwards, with the uropods touching the floor of the tube. The peduncle of the first pair of uropods is at an angle to the others, and its rami point forwards. The first two pairs of peraeopods have their claws and carpal joints resting on the floor of the tube, and are never at rest, always stamping at it. The second gnathopod has its first two joints vertical, with the remainder horizontal. Its position is more fully described below. The last three pairs of peraeopods are bent back over the metasome, in the position characteristic of so many other amphipods, with their claws hooked into the wall of the tube. About once every thirty seconds, or as often as the animal is alarmed, the metasome is still further arched, withdrawing the head, while the peraeopods push against the tube, causing the animal to turn a neat backwards somersault so that its head appears at the other entrance. The same reversal of position has been described in *Amphithöe*.

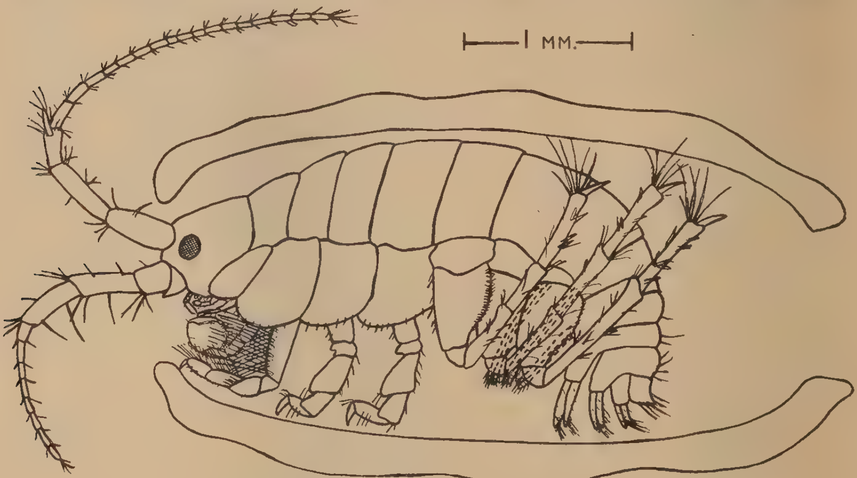


Fig. 2. *Leptocheirus pilosus* ♂. Position in the tube.

Feeding Habits

Hart (1930) and others have recognized three types of amphipod feeding:

(1) Biting, e.g. *Talitrus*, *Lysianassa*, *Amphithöe*, etc.
(2) Selective deposit feeding, e.g. *Corophium*.
(3) Filter feeding, e.g. Haustoriidae.

Leptocheirus pilosus belongs to the second class. Its mouthparts are in all essentials similar to the biting mouthparts of *Amphithöe*. The mandibles have molar processes, and the other parts do not have the specialized fringes of pinnate setae described by Dennell (1933) in *Haustorius arenarius* which is a true filter feeder. Any feeding current is not produced by the mouthparts. A stream of water is, however, induced to flow from the head to the telson by the beating of the pleopods. Since the animal is in a tube, the water cannot flow in at the sides and a strong current through the entrance is thus produced. Any solid particles are sieved (this is a better word than filtered) out of the stream by a special arrangement of setae on the second gnathopod.

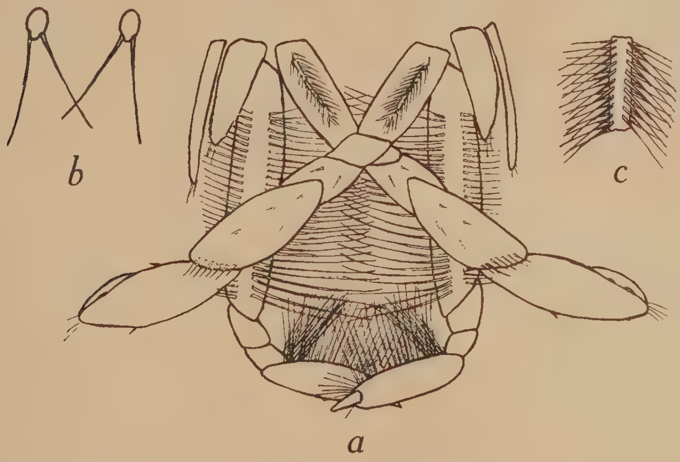


Fig. 3. *Leptocheirus pilosus* ♂. *a*, First and second gnathopods in their normal positions seen from in front, to show the arrangement of sieve setae. *b*, Diagram of a transverse section through the basal joint of the second pair of gnathopods, showing the two rows of sieve setae. *c*, Part of a sieve seta. Magnified.

On the anterior face of the basal (1st) joint of this limb there are two rows of very long feathery setae. The outer row is parallel with the walls of the tube, while the inner points inwards at an angle of about 30° (Fig. 3*b*). The ends of the setae of this inner row cross in the middle with those on the opposite gnathopod forming a fine sieve through which the stream flowing down the tube must pass. There are single rows of similar setae projecting upwards and inwards from the horizontal meral and carpal joints, and there is thus an enclosed space behind the first pair of gnathopods and under the mouth. This is closed posteriorly by the two inner rows on the basal joints, laterally by the outer rows on these joints, and dorsally and ventrally by the head, and setae of the meral and carpal joints respectively. Any solid suspended matter in the food stream is caught in this space. Periodically the second gnathopod is bent at the ischial joint, and the distal segments are lifted up into the space between the two rows of setae on the basipodite. Any particles caught in these setae are combed off into the enclosed space by those on the distal joints of the limb. The detritus in this space is turned over by the maxillipeds, assisted by the first pair of gnathopods in the female, and any suitable particles are transferred to the mouth. This method of food collection, for which the term sieve feeding is proposed, is quite different from the filter feeding of *Haustorius arenarius* and many other animals. In the latter, water having various food particles in suspension is drawn through the mouth appendages, which are highly specialized, both creating the feeding current and performing the filtration. In the sieve feeder the creation of the feeding current and the extraction of food particles from it are performed by appendages other than those of the head, and the food materials so collected are offered to the mouth-parts as a loosely concentrated mass of detritus, in much the same state as is the food of any other selective deposit feeder. The mouthparts are in no way specialized for filter feeding and a sieve feeder, such as *Leptocheirus* could not be classed with *Haustorius*, but rather with *Corophium* and the other selective deposit feeders.

Besides sieve feeding *Leptocheirus pilosus* can also behave as a normal selective deposit feeder. If any large mass of detritus is perceived near the mouth of the tube by the sensory antennules, the animal will partially emerge from the tube, grasp at it with the antennae, which have long and stout setae on the ventral sides of the peduncular joints, and draw it into the mouth of the tube. In neither sex are the gnathopods used to grab at food, as in *Amphithöe*. This method of collecting food was often seen in animals in the tubes on the bottom of a glass dish, where there was plenty of detritus lying round the nest. It is probably used by the occupants of nests on flat stones near the bottom of the pond, but when the tubes are on *Chondrus crispus* some distance above the bottom, large masses of food which could be taken in by the antennae would not be common, and it is probable that the sieve method is then the most usual.

Leptocheirus pilosus never gnaws at such algae as *Ulva* or *Enteromorpha*, as does *Amphithöe*. It will die if it is put in a dish containing nothing but such an alga. The contents of the gut consist entirely of very small particles, diatoms and very small lengths of algal filaments being recognizable.

The feeding habits of *Leptocheirus pilosus* are thus entirely different from those observed by Holmes and Skutch for *Amphithöe*, which has no adaptations for sieve feeding, and is often carnivorous. Hart describes a very much more simplified form of sieve feeding in *Corophium volutator*, which possesses a single row of setae on the distal joints of the first pair of gnathopods; but *Corophium* is primarily a true selective deposit feeder, and does not use these setae to any great extent.

Most of the material which enters the space in front of the sieve setae is not used as food. Part of it is worked into the walls of the tube by the first and second peraeopods. The rest is left behind when the animal somersaults round, and is then kicked out of the entrance of the tube by the urosome, which appears at this end. No solid particles are allowed to get past the second gnathopods, and so the tube is kept clear of particles which might, in very dirty water, block it up. The faeces are disposed of in the same way.

The tubes on the *Chondrus* fronds are exposed for several hours at each tide. The animals remain in them, and water is held in the tube by capillarity. When thus exposed the pleopods beat gently, keeping up a circulation of the water in the nest, which is thus able to aerate the branchial lamellae with the oxygen which presumably diffuses into the water at each end of the tube. The antennae and antennules are withdrawn, and the animal no longer performs its frequent changes of position. If it is removed from its tube when out of the water it is not able to break the surface film when the *Chondrus* plant is reimmersed. Under natural conditions however, it remains in its tube, and is thus never out of water.

Leptocheirus pilosus is able to swim quite efficiently, unlike *Amphithöe* which, if removed from its nest, will lie on the bottom, grasping at any solid object which is there. *Leptocheirus pilosus* will usually, however, enter a vacant tube, or build a new one as soon as possible. It may eject another individual from its tube, if it can enter the tube from behind before the occupant has time to reverse its position and face the intruder. If it can get in from behind, the rightful owner is easily pushed out. It cannot, however, be ejected if it is facing the intruder. *L. pilosus* will seldom leave its tube spontaneously, though a few individuals can be caught if a net is drawn gently over the *Chondrus* plants. Since any disturbance causes the animal to retreat further into its tube, these few must probably have been swimming about freely.

Breeding Habits and Life History

No attempt to go very deeply into this question was made, and further work on the breeding habits of amphipods in general is contemplated. In the meantime the few observations which were made may be recorded.

Ovigerous females were obtained from the beginning of April till September inclusive. These on the average carried eleven eggs each, and very few individuals were found with more or less than this number. The number is just half that given by Chevreux, but this may be due to climatic or other factors.

There was a great preponderance of females over males during the whole time the species was under observation, and the relative numbers did not appear to fluctuate much. A collection of fifty-eight made in August contained seven males and thirty-six females, with fifteen too young for their sex to be recognized.

Two adult individuals were never observed together in one nest, and indeed there would not be enough room in any ordinary one. According to Skutch a male and female *Amphithöe rubricata* are often found together. Only one copulating pair was observed, and this was outside the nest. It was examined under a hand lens, and the male seemed to be holding his mate with the second gnathopods and anterior peraeopods. The first gnathopods were crossed under the body in the usual position, and were not used in the clasp. The peculiar carriage of these limbs does not seem to be explicable as a clasping adaptation. The pair separated when being transferred to another dish for further observation under the microscope, and this would seem to cast some doubt on whether they were really copulating, since the clasp is usually extremely tenacious.

In some species of Amphipoda, *Haustorius arenarius* investigated by Dennell (1933) and *Corophium bonelli*, by Crawford (1937) and a few others, the male is unknown, and reproduction is presumably parthenogenetic. No experiments were undertaken to determine whether this was so with *Leptocheirus pilosus*, either as a general rule or occasionally, but the single and rather doubtful observation of a copulating pair, together with the disproportionate sex ratio suggest that parthenogenesis may occur. In most amphipods clasping pairs are very noticeable throughout the breeding season.

As in most species the young remain in the brood pouch until after the first moult, while they remain in the tube of the mother until the second, and possibly later. On leaving they soon construct their own tubes. Moulting is normal, the animal emerging from a dorsal crack just behind the head and leaving the old skin otherwise unbroken. The moult always occurs outside a tube, and if the animal has grown during the process it probably builds a completely new tube.

CONCLUSION

In its general behaviour *Leptocheirus pilosus* occupies a position between *Corophium volutator* and *Amphithöe rubricata*. It is able to swim efficiently, unlike *A. rubricata*, but it appears that it does not habitually leave the nest, as does *Corophium volutator*. The nest is a true one, not a mere burrow in the mud, but in its cementing it resembles the burrow of *C. volutator*. The secretion of silken threads for the construction of the nest is not found, and the cement glands are not confined to the first two peraeopods, as in *Amphithöe rubricata*.

The sieve-feeding mechanism is an interesting adaptation to the tubicolous existence, which does not appear previously to have been recorded in the Amphipoda. In this respect *Leptocheirus pilosus* is probably more highly specialized than are the other tube-building forms. *Amphithöe* has both pairs of gnathopods grasping and subequal, and seizes the food with them in the same way as do such free swimming genera as *Gammarus*. It must partly emerge from its tube in order to grasp at passing food masses, and has no means of feeding while it is inside the tube. *Corophium volutator* has a single row of primitive sieving setae on the posterior border of its first gnathopod, which are analogous to the double row on the anterior border of the second gnathopod of *Leptocheirus pilosus*. It obtains its food more frequently, however, in the normal manner of other detritus feeders, and its sieving mechanism is not so highly developed as that of *Leptocheirus pilosus*.

This sieve feeding is analogous to the true filter feeding of *Haustorius arenarius* (Dennell, 1933), and the mysids. In these the collection of food particles, and creation of the food current, are both performed by specialized mouthparts, while in *Leptocheirus pilosus* this is done by the appendages of the meso- and metasome, and the mouthparts are of the unspecialized biting type. Since the animal lives in a tube, the current produced by the pleopods is bound to flow down the tube and over the sieving setae; it cannot get in at the sides, nor from underneath behind the second gnathopod, as would happen if there were no tube. It can therefore do its sieving on a larger scale than can the mysids or *Haustorius arenarius*, whose food current is of a much smaller capacity, and is produced by the mouthparts in an enclosed space which, since there is no tube, can only be provided by a fold of the carapace, or by the walls of pinnate setae through which water cannot easily pass. No comments will be made on the breeding habits of *Leptocheirus pilosus* until further experimental evidence has been obtained.

I wish to express my thanks to Mr D. M. Reid, for his valued help and criticism of this work.

SUMMARY

A study made of the adaptations to tubicolous life found in the small brackish water Photid Amphipod, *Leptocheirus pilosus* Zaddach, revealed several interesting points.

The presence of cement glands in many amphipods has been recognized by several previous authors. In *L. pilosus* these glands are found mainly in the upper joints of the first two pairs of peraeopods, opening to the exterior through a common duct in the claw. Unicellular glands are also found all over the body, particularly on the coxal plates.

The tubes of amphipods are of four main types:

(1) Sand burrow, e.g. Talitridae, *Ampelisca*.
(2) Mud burrow, e.g. *Corophium volutator*.
(3) Homogeneous leathery tube, e.g. *Leptocheirus pilosus*.
(4) Nest of algal fragments, bound together by "amphipod silk", e.g. *Amphithöe rubricata* and *A. longimana*.

The third type has not previously been described. It consists of a short, flat blister-like capsule fixed to a flat surface, usually the alga *Chondrus crispus*, and is built of minute particles of detritus cemented firmly together with a secretion from the dermal glands. Experiments showed that *Leptocheirus pilosus* could rapidly make a normal tube, both from natural and combusted detritus. If supplied only with fragments of *Ulva*, or sand grains, a very fragile tube was eventually constructed, the parts being fixed together by weak strands of mucus. No "amphipod silk" was used. An animal from

which the 1st and 2nd pairs of gland-bearing peraeopods have been removed is unable to build a tube.

Leptocheirus pilosus collects its food by the method of sieving. A stream of water, created by the pleopods, flows down the tube and any solid particles suspended in it are collected by an arrangement of long setae on the second pair of gnathopods. From the mass of detritus thus collected, suitable food particles are selected by the mouthparts. The remainder is incorporated into the wall of the tube from the inside. This method of feeding is of the selective deposit type, and does not resemble the filter feeding found in some species. The animal is able also to draw into the tube masses of detritus with the antennae, but it does not gnaw at large pieces of an alga, nor is it carnivorous.

From the scanty observations made, the breeding habits of the species do not appear to be normal. There is a great preponderance of females and the occurrence of copulation is doubtful. The peculiar carriage of the well developed first pair of gnathopods by the male does not appear to be an adaptation for pairing, and no explanation for it is put forward. It is tentatively suggested that the species may be parthenogenetic.

The young remain in the mother's brood pouch until after the first moult, and remain in her tube for some time after this. On leaving it they forthwith build tubes of their own.

REFERENCES

Calman, W. T., 1909. Crustacea; in *A Treatise on Zoology*, ed. Sir R. Lankester, 7 Appendiculata 3rd Fasc., pp. 235–6. London.

Chevreux, E. & Fage, L., 1925. *Faune de France*, Vol. 9. Amphipodes, pp. 322–3.

Claus, C., 1879. Der Organismus der Phronimiden. *Arbeit Zool. Instit. Wien*, Bd. ii, pp. 59–88.

Crawford, G. I., 1937. A review of the amphipod genus *Corophium*, with notes on the British species. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 589–630.

Dennell, R., 1933. The habits and feeding mechanism of the amphipod *Haustorius arenarius* Slabber. *Journ. Linn. Soc. Zool. London*, Vol. xxxviii, pp. 363–88.

Hart, T. J., 1930. Preliminary notes on the bionomics of the amphipod *Corophium volutator* Pallas. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 761–89.

Holmes, S. J., 1901. Observations on the habits and natural history of *Amphithöe longimana* Smith. *Biol. Bull.*, Vol. ii, pp. 165–93.

Hunt, O. D., 1925. The food of the bottom fauna of the Plymouth fishing grounds. *Journ. Mar. Biol. Assoc.*, Vol. xiii, pp. 560–99.

Reid, D. M., 1938. Burrowing methods of *Talorchestia deshayesii* Audouin. *Ann. Mag. Nat. Hist.*, Ser. 11, Vol. i, pp. 155–7.

Schellenberg, A., 1929. Körperbau und Grabweise einiger Amphipoden. *Zool. Anz.*, Leipzig, Bd. lxxxv, pp. 186–90.

Sexton, E. W., 1911. On the amphipod genus *Leptocheirus*. *Proc. Zool. Soc. London*, pp. 561–94.

Skutch, A. F., 1926. On the habits and ecology of the tube-building amphipod *Amphithöe rubricata* Montagu. *Ecology*, Brooklyn, N.Y., Vol. vii, pp. 481–502.

SMITH, S. J., 1874. Tube building Amphipoda. *Amer. Journ. Sci.*, Ser. 3, Vol. VII, p. 601.

— 1882. On the amphipodous genera *Cerapus*, *Unciola* and *Lepidactylis*. *Trans. Conn. Acad. Arts Sci.*, Vol. IV, pp. 268–84.

STEBBING, T. R. R., 1906. Amphipoda I. Gammaridea. *Das Tierreich*, Vol. XXI. Berlin.

STEPHENSEN, K., 1929. *Die Tierwelt der Nord- und Ost-See*, Bd. XIV, X, f. Amphipoda, pp. 13, 159.

ZAVATTARI, E., 1920. Osservazioni etologiche sopra l' anfipodo tubicolo *Ericthonius brasiliensis* Dana. *R. Comm. Talassogr. Ital.*, Mem. 142. Venezia. Ferrari 8°, p. 22.

SOME NEW SAND-DWELLING COPEPODS

By A. G. Nicholls, Ph.D.

Marine Station, Millport

(Text-figs. 1–7)

The copepods described in this paper come from two sources, the Firth of Clyde and the St Lawrence River. Several new species were collected from Balloch Bay on the Greater Cumbrae in 1935 and 1936 during an attempt to obtain some of the early species described from Scottish waters. The remainder were collected while working at the Biological Station at Trois Pistoles, Quebec, during a visit to Canada in 1937. The environment in Balloch Bay is composed of a fine muddy sand, strewn with boulders. The bay is on the eastern side of the island and therefore in a sheltered position. A description is given in Appendix III of *The Biology of the Sea Shore*, by Flattely & Walton (1922). The conditions under which the Canadian material was found will be dealt with in a later paper describing the remainder of the collection from the St Lawrence; it will be sufficient here to state that the conditions are essentially marine.

Copepods from three allied genera are included here: *Paramesochra* T. Scott, 1892; *Leptopsyllus* T. Scott, 1894; and *Remanea* Klie, 1929. The first two have for some time been in a state of considerable confusion and it has been a matter of some doubt into which genus the various species should be placed. Several efforts have been made to clarify the position (notably by Klie, 1929 and Monard, 1935) but the more recent work of Kunz (1938) has produced a clear separation based on the presence or absence of an endopod on the second leg. When the variation in the structure of the endopods of the second, third and fourth legs is studied in these two genera it becomes apparent that such a separation is far from natural, but it will suffice until a thorough revision of these and allied genera has been made. In an earlier paper (1935) I suggested that the genus *Emertonia* of Wilson (1932) was in reality a synonym of *Leptopsyllus*. Kunz (1938) points out that it has enough distinct characters to render it a valid genus and with this opinion I must for the present agree.

Klie (1929) included *Leptopsyllus* and *Paramesochra* in a single genus and for this view there is much support since there is a considerable overlapping between the two. Moreover, *Leptopsyllus littoralis* n.sp. is intermediate between *Emertonia* and *Leptopsyllus*, resembling the former in the possession of a 1-segmented exopod in the first leg but differing from it in the absence of endopods on legs 2–4.

Included in this paper are keys to the genera *Paramesochra* and *Leptopsyllus* based on those of Kunz, and extended to include the new species here described.

The following abbreviations have been used in the figures:

*a.*1.	first antenna.	*a.*2.	second antenna.	*c.r.*	caudal rami.
g.a.	genital area (♀).	*U.*	urosome.	*md.*	mandible.
mxl.	maxillule.	*mx.*	maxilla.	*mxp.*	maxilliped.
		I, II, III, IV, V, and VI.	Legs 1–6.		

Genus Leptopsyllus T. Scott, 1894

As stated above, this genus has now been modified and includes only those forms which lack endopods on the second legs.

KEY TO THE SPECIES

1.	Third endopod absent	2
	Third endopod present, 1-segmented	*arcticus* (Lang) 1936
2.	Fourth endopod absent	3
	Fourth endopod present, 1- or 2-segmented	4
3.	First exopod 1-segmented	*littoralis* n.sp.
	First exopod 2-segmented	*spinipes* n.sp.
4.	Fourth endopod 1-segmented	*paratypicus* n.sp.
	Fourth endopod 2-segmented	*typicus* T. Scott, 1894

Leptopsyllus littoralis n.sp. (Fig. 1).

Occurrence. Balloch Bay, Firth of Clyde; washed from sand at about half-tide level, at a depth of between 7 and 10 cm.

Female. Length 0·48 mm. Body tapering only slightly, somewhat constricted between segments. First antenna 9-segmented, the first two segments the largest; second antenna with the usual 3-segmented endopod and 1-segmented exopod, the latter with two terminal and two lateral setae. Mouth parts of generic type. First leg with 1-segmented exopod and 2-segmented endopod; exopod bearing four terminal and one lateral setae, with numerous small marginal setae; endopod with two large and one small setae at end of distal segment. Legs 2–4 all with 3-segmented exopods and no endopods. Fifth legs with distal segments fused with basal segment, the basal segments of opposite sides being fused in the mid-line and expanded into the usual lamella, which overlaps the genital area and is without setae; distal segments prolonged into spines and bearing four setae of which three are situated outside the spine. Caudal rami twice as long as wide and about two-thirds as long as anal segment. Egg-sac single with five or six spherical eggs carried one behind the other.

Male. Length 0·41 mm. First antenna 6-segmented; legs 1–4 almost iden-

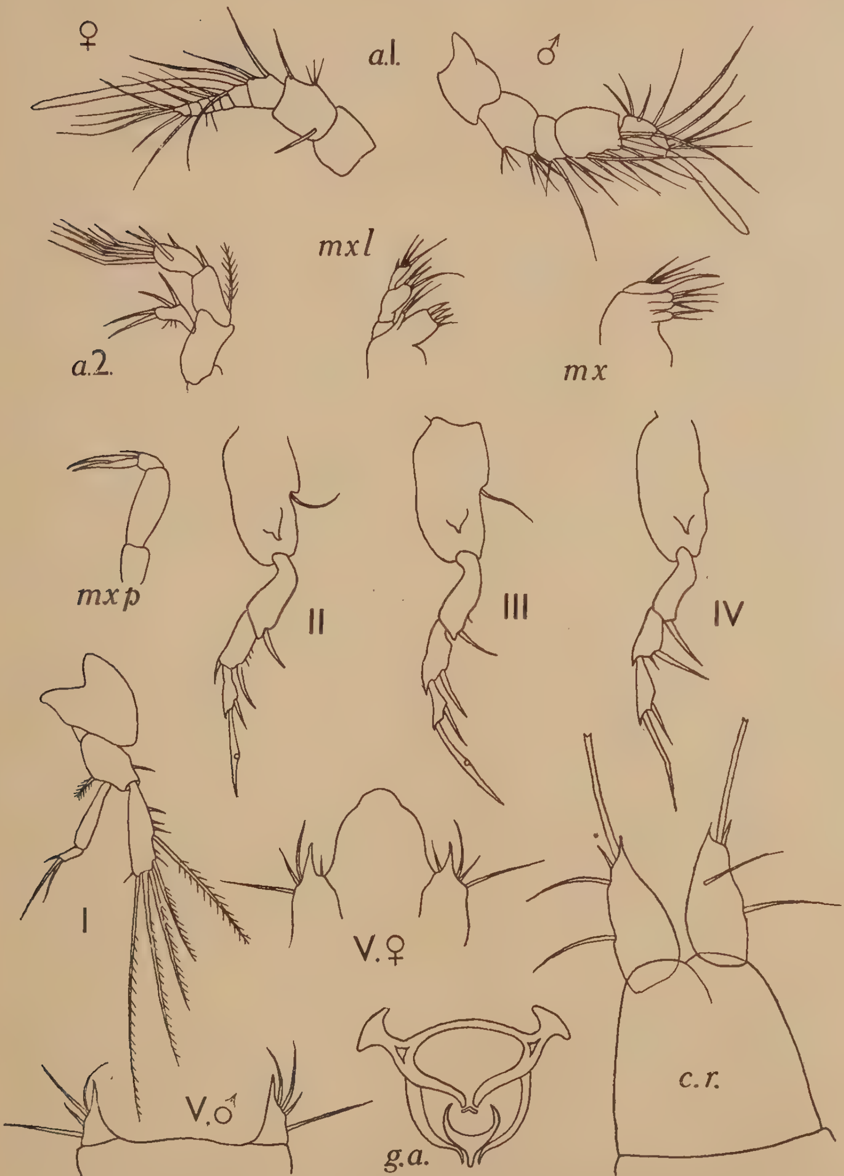

♀
a.l.
♂
a.2.
mxl
mx
mxp
II
III
IV
I
V.♀
V.♂
g.a.
c.r.

Fig. 1. *Leptopsyllus littoralis* n.sp. The figures are all drawn to the same scale.

tical with those of the female; 5th legs similar to those of female but without the large basal expansion.

This species resembles *Emertonia gracilis* Wilson (1932) in the structure of the first pair of legs, though the proportions of the segments of the endopod differ; it also differs from this and from previously described species of *Leptopsyllus* in lacking endopods on three pairs of legs, the second, third and fourth, and in the structure of the fifth legs.

Leptopsyllus spinipes n.sp. (Fig. 2).

Occurrence. Balloch Bay, Firth of Clyde; washed from sand near low-water springs, down to a depth of 10 cm.

Female. Length 0·43 mm. Body of usual form, moderately constricted between segments; urosome 4-segmented. Rostrum small; first antenna 7-segmented, the basal segment the largest; second antenna with 1-segmented exopod bearing two terminal and one lateral seta. Mouth parts of the usual structure. First legs with 2-segmented rami, endopod longer than exopod and tipped with two setae. Legs 2–4 with 3-segmented exopods and no endopods. Fifth legs of opposite sides fused in mid-line but basal segment not greatly expanded and ending in three pointed lobes; distal segments distinct, with two setae. Caudal rami as wide as long, subtriangular in shape, forming flattened plates armed with several short spines and setae.

Male. Length 0·36 mm. Body similar to that of female; urosome 5-segmented. First antenna 7-segmented, the 3rd segment bearing a relatively large curved spine. Legs 1–4 identical with those of female; fifth legs without inner basal expansion, distal segments with three setae; sixth legs with small basal expansion. Caudal rami somewhat longer than in female (half as long again as wide) and with fairly long terminal setae.

This species resembles *L. littoralis* in the absence of 2nd, 3rd and 4th endopods, but differs in the structure of 1st and 5th legs and caudal rami. The caudal rami of the male of this species are rather different from those of the female, which were probably slightly compressed while being drawn.

Leptopsyllus paratypicus n.sp. (Fig. 3).

Occurrence. Balloch Bay, Firth of Clyde; washed from sand.

Female. Unknown.

Male. Length 0·36 mm. Body of usual form, with 5-segmented urosome. First antenna 5-segmented, bearing aesthetascs on 4th and 5th segments; 2nd antennae with 1-segmented exopods bearing three terminal and one lateral seta. First legs with 2-segmented rami, the endopods slightly longer than the exopods. Second and third legs alike, with 3-segmented exopods and no endopods. Fourth legs with 3-segmented exopods and 1-segmented endopods, armed with a single large terminal spine. Fifth legs with basal segments of opposite sides fused in mid-line but not expanded; distal segments

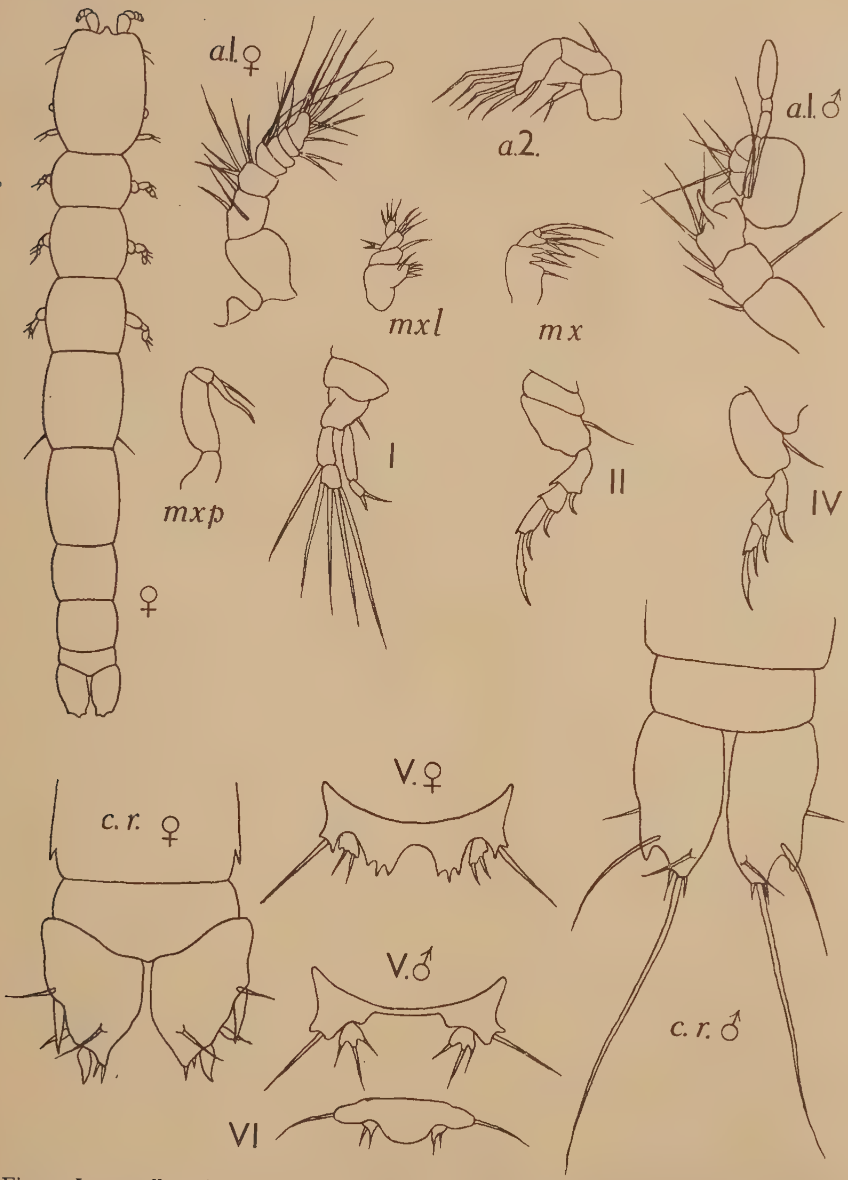

a.l.♀
a.2.
a.l.♂
mxl
mx
mxp
I
II
IV
♀
c.r. ♀
V.♀
V.♂
VI
c.r.♂

Fig. 2. *Leptopsyllus spinipes* n.sp. The figures are all drawn to the same scale except the dorsal view of the female which is less highly magnified.

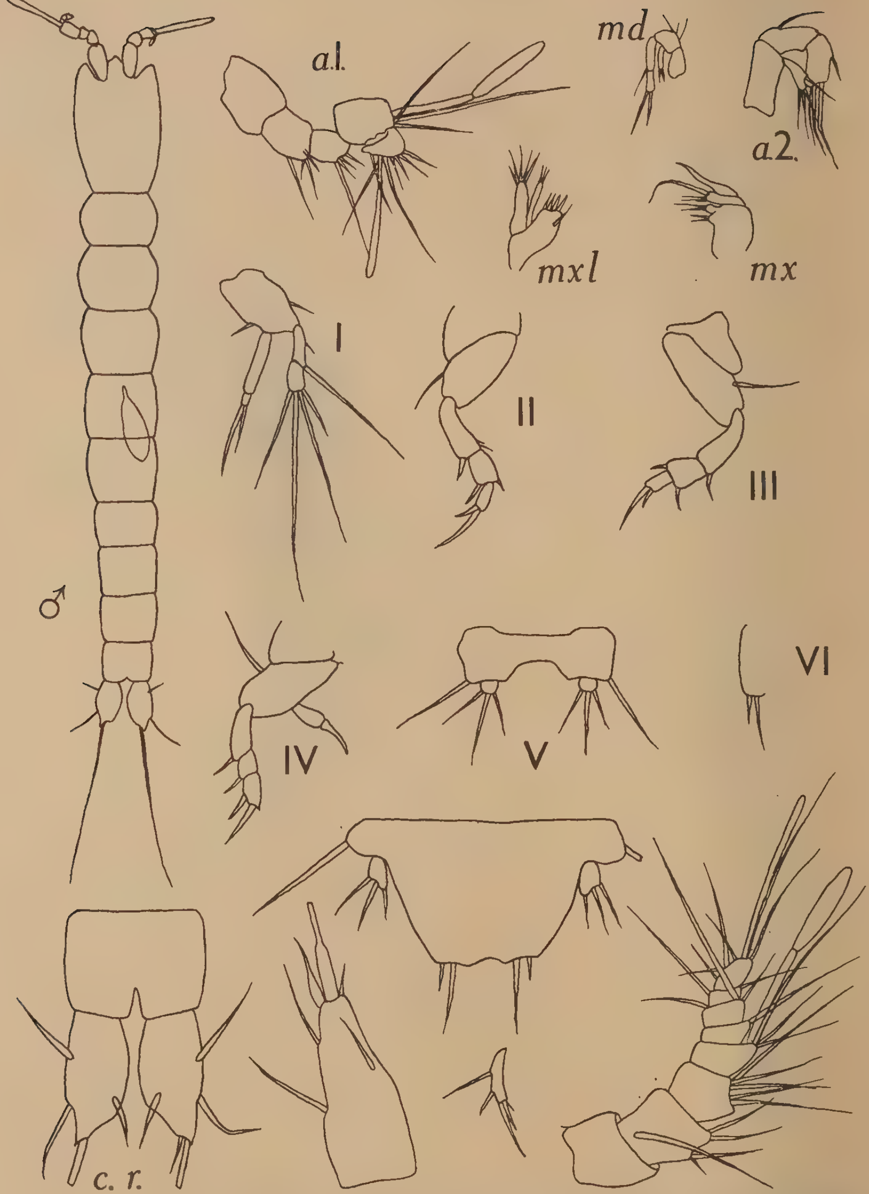

a.l.
md
a2.
mxl
mx
I
II
III
♂
IV
V
VI
c. r.

Fig. 3. *Leptopsyllus paratypicus* n.sp. Male only. The unlabelled figures are those of the first antenna, exopod of the second antenna, fifth legs, and caudal ramus of the female of *Paramesochra minor* (T. & A. Scott). All to the same scale.

with three long setae. Caudal rami twice as long as wide and a little longer than the anal segment, armed with one long and one short terminal seta and three other setae.

This species resembles *L. typicus*, of which only the female has been described, in having no endopods on the 2nd and 3rd legs but differs from it in having only 1-segmented endopods on the 4th legs and in the armature of the caudal rami. The great difference in size (0·74 and 0·36 mm.) also rules out the possibility of this being the male of *L. typicus*.

Genus Paramesochra T. Scott, 1892

Key to the Species

1.	Fourth exopod 2-segmented	2
	Fourth exopod 3-segmented	4
2.	Second exopod 3-segmented	3
	Second exopod 2-segmented	*laurentica* n.sp.
3.	Second endopod 2-segmented	*intermedia* (T. & A. Scott) 1895*a*
	Second endopod 1-segmented	*minuta* n.sp.
4.	Basal segment of 1st antenna strongly hooked distally	*dubia* T. Scott, 1892
	Basal segment of 1st antenna not hooked	5
5.	Anal segment with lateral backwardly projecting points	*pterocaudata* Kunz, 1937
	Anal segment without such points	6
6.	Fourth endopod 1-segmented	7
	Fourth endopod 2-segmented	11
7.	Caudal rami without inner setae	8
	Caudal rami with an inner dorsal seta	9
8.	Caudal ramus with a stout spine at outer distal corner	*holsatica* Klie, 1929
	Caudal ramus with plumose seta in place of spine	*pygmaea* n.sp.
9.	First endopod 1-segmented	*constricta* (Nicholls) 1935
	First endopod 2-segmented	10
10.	First endopod with large curved spine and one seta on terminal segment which is one-quarter of basal segment; size 0·40–0·46 mm. (♂ only)	*coelebs* (Monard) 1935
	First endopod with two spines on terminal segment which is one-third of basal segment; size 0·70 mm. (♂ used for comparison)	*major* n.sp.
11.	Caudal ramus prolonged into a point posteriorly; end segment of 4th exopod with three setae; basal expansion of 5th leg tapering to a point	*acutata* Klie, 1934
	Caudal ramus not pointed posteriorly; end segment of 4th exopod with two setae; basal expansion of 5th legs rounded, with two setae	12
12.	Basal segment of 4th endopod without setae	13
	Basal segment of 4th endopod with an inner seta	15
13.	Second endopod without setae	14
	Second endopod tipped with one seta	*herdmani* (Thompson & Scott) 1900

14. Caudal rami three times as long as wide; 1st exopod as long as whole endopod; size about 0·63 mm. ... *robertsoni* (T. & A. Scott) 1895*b*
Caudal rami 2–2½ times as long as wide; 1st exopod no longer than basal endopod; size 0·33–0·46 mm.... ... ... *minor* (T. & A. Scott) 1895*b*

15. Basal segment of 3rd endopod with one inner seta; end segments of 5th legs rounded, bearing setae only ... ... *similis* Kunz, 1937
Basal segment of 3rd endopod without setae; end segment of 5th leg tapering to end in a large spine ... ... *helgolandica* Kunz, 1937

Paramesochra minor (T. & A. Scott) 1895*b* (see Fig. 3).

Occurrence. Trois Pistoles, St Lawrence River; washed from coarse sand near seaward end of breakwater, at a depth of between 5 and 8 cm.

Distribution. Musselburgh, Firth of Forth; Kames Bay, Millport, Firth of Clyde; Kiel Bay, Germany.

A few specimens of this copepod were obtained near the breakwater at Trois Pistoles, Quebec, which differ in only small points from previous descriptions. The first antennae are 8-segmented in the female; the exopod of the 2nd antenna has three terminal and two lateral setae; the general proportions of the 5th legs are similar but the shape of the basal expansion is not quite the same; and the setae of the caudal rami do not quite correspond. These small differences do not justify a new species. It is remarkable that this species should be so widely distributed when it is customary among these sand-dwellers to find entirely different species in adjacent bays.

Paramesochra pygmaea n.sp. (Fig. 4).

Occurrence. Balloch Bay, Firth of Clyde; washed from sand near low-water springs, down to a depth of 10 cm.

Female. Length 0·25 mm. Body distinctly tapering posteriorly, somewhat constricted intersegmentally in the metasome; urosome 4-segmented. First antenna 7-segmented, basal segment the largest; 2nd antenna with 1-segmented exopod armed with one terminal and two lateral setae. First legs with 2-segmented rami; endopod nearly half as long again as exopod; endopod with two terminal setae, exopod with four terminal setae. Second and third legs identical, with 3-segmented exopods and 1-segmented endopods, the latter somewhat swollen distally and bearing each a single small terminal plumose seta; distal exopod segment bearing three spines and one plumose seta. Fourth legs similar to 2nd and 3rd but lacking the terminal plumose seta on the exopods. Basal expansions of 5th legs large and almost completely fused in the mid-line, with two terminal setae on each side; distal segments with five setae. Caudal rami slightly more than twice as long as wide and about half as long again as anal segment, bearing three unequal setae terminally and one lateral seta.

Male. Length 0·24 mm. Body similar to that of the female but with 5-segmented urosome. First antenna 5-segmented, with a short stout aesthetasc on the 4th segment. Legs 1–4 identical with those of female; 5th legs with basal expansion scarcely extending beyond end of distal segments and without terminal setae; distal segment with one long spine and three short setae.

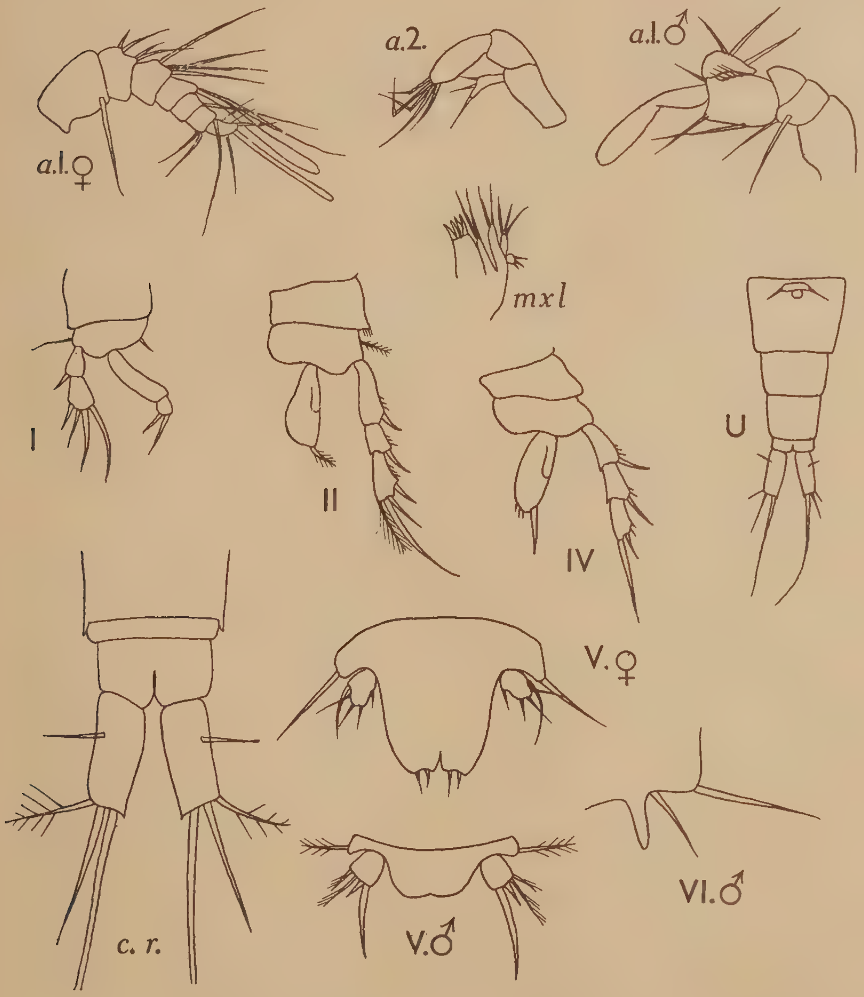


Fig. 4. *Paramesochra pygmaea* n.sp. Except for the urosome of the female the drawings are all to the same scale.

This species resembles *P. holsatica* in the general structure of its legs and in its small size, but can be distinguished easily by the presence of a small plumose seta at the outer corner of the caudal ramus in place of the stout spine in *holsatica*.

Paramesochra minuta n.sp. (Fig. 5).

Occurrence. Balloch Bay, Firth of Clyde; washed from sand.

Female. Length 0·38 mm. Body not tapering very much; urosome 4-segmented, anal segment very short. First antenna 8-segmented; exopod of 2nd antenna 1-segmented with two terminal and one lateral seta. First legs with 2-segmented rami about equal in length or the exopod slightly the longer. Legs 2 and 3 with 3-segmented exopods and 1-segmented endopods, the latter somewhat narrowed distally and bearing only three short hairs. Fourth legs with 2-segmented exopods and 1-segmented endopods, not constricted terminally but bearing a single large spine. Fifth legs with very large basal expansions entirely fused and semi-circular in outline, with one seta on each side; distal segments very small and fused with basal segments, distinguishable only as small knobs each bearing two setae. Caudal rami twice as long as wide and about half as long again as the anal segment.

Male. Unknown.

This species resembles *P. intermedia* in several particulars but differs in size, in the structure of the 2nd endopods and of the 5th legs.

Paramesochra major n.sp. (Fig. 6).

Occurrence. Baie de Mille Vaches, St Lawrence River; washed from very coarse sand taken by grab in a depth of 8 m.; numerous specimens.

Female. Length 0·80 mm. Body with metasome wider than urosome, tapering gradually posteriorly; urosome 4-segmented. First antenna 9-segmented, basal segment the largest. Second antenna with 1-segmented exopod bearing one terminal and two lateral setae and two small hairs. First legs with 2-segmented rami, the endopod about twice as long as the exopod and with its distal segment not always clearly separated from the basal segment, the latter about five times as long as the end segment. Legs 2–4 with 3-segmented exopods and 1-segmented endopods. The distal segment of the 2nd exopod with three spines and one plumose seta, of 3rd exopod with two spines and one plumose seta (the proximal spine being absent) and of 4th exopod with two spines only. Second and third endopods rounded, with one terminal plumose seta; 4th endopod tapering, with one stout spine. Fifth legs with basal expansions fused for two-thirds of their length, bearing two setae; distal segments small, with three setae. Caudal rami three times as long as wide and twice as long as anal segment. Egg-sac single, with 9–10 eggs.

Male. Length 0·70 mm. Body similar to that of female; urosome 5-segmented. First antenna 6-segmented with a short stout aesthetasc on 4th segment. First leg as in female but with basal endopod segment only three times as long as distal segment. Second and third legs similar and like 2nd leg

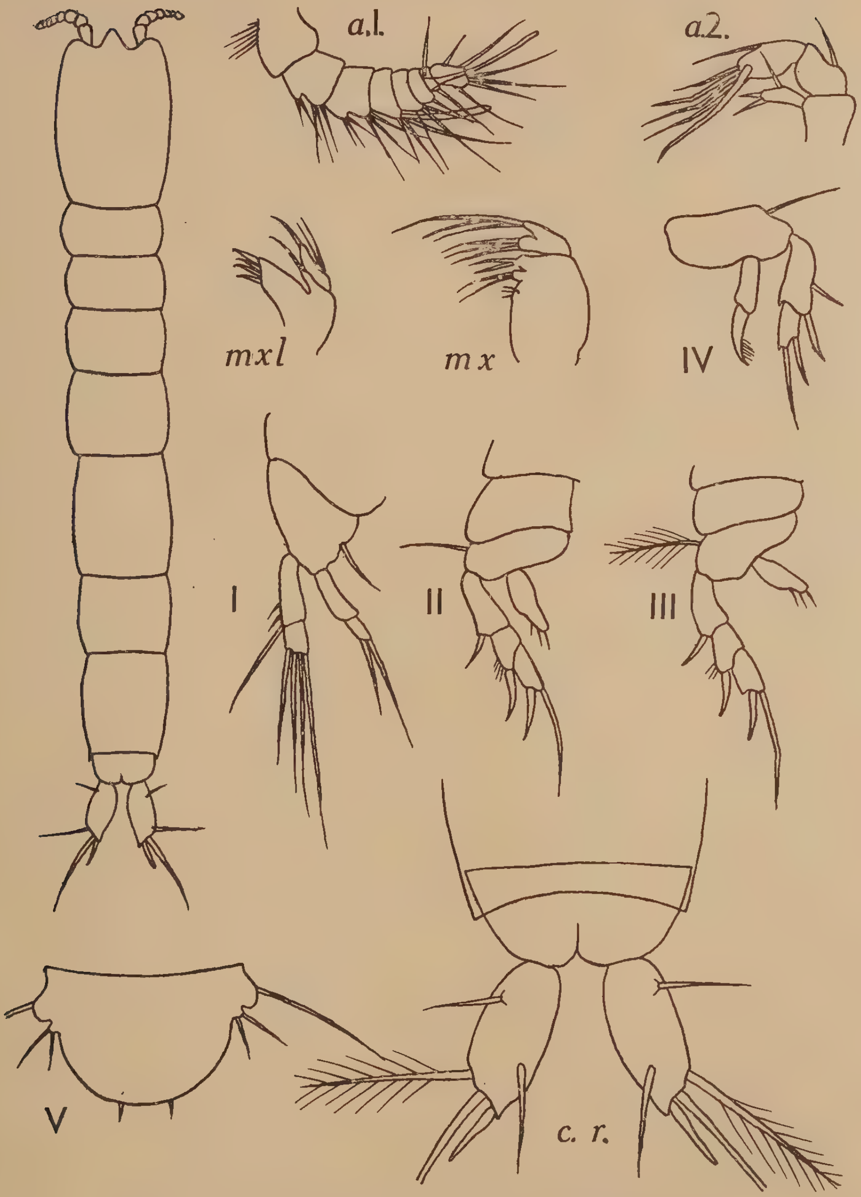

a.l.
a2.
mxl
mx
IV
I
II
III
V
c. r.

Fig. 5. *Paramesochra minuta* n.sp. Female only. All to the same scale except for the dorsal view of the adult.

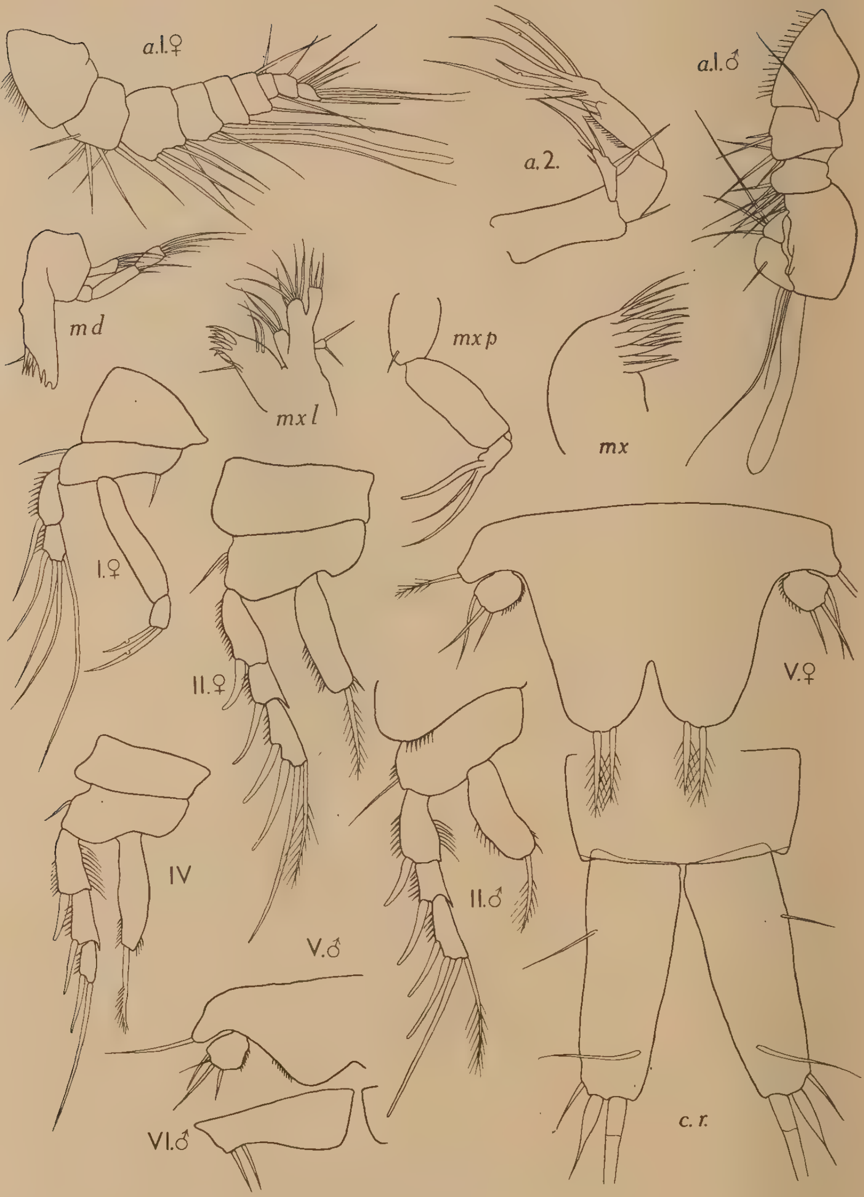

a.l.♀
a. 2.
a.l.♂
md
mxl
mxp
mx
I.♀
II.♀
V.♀
IV
II.♂
V.♂
VI.♂
c. r.

Fig. 6. *Paramesochra major* n.sp. All figures drawn to the same scale.

of female. Fourth legs like those of female. Fifth legs with small basal expansion, without setae; distal segment with four setae. Caudal rami like those of female.

This species is the largest yet described belonging to this genus, though *Leptopsyllus typicus* is nearly as large, and although resembling *Paramesochra coelebs* (only the male of which is known) is quite easily separated by the difference in the 1st legs and in the size.

Paramesochra laurentica n.sp. (Fig. 7).

Occurrence. Baie de Mille Vaches, St Lawrence River; washed from coarse sand taken by grab from 8 m. One specimen only.

Female. Length not known. First antenna 7-segmented, the 3rd the largest. Second antenna apparently without an exopod but this may have been lost in dissection. First leg with 2-segmented rami, endopod nearly twice as long as exopod. Legs 2–4 with 2-segmented exopods and 1-segmented endopods, the latter with a single seta in 2nd and 3rd legs and with a single stout spine in 4th legs. Distal segments of 2nd and 3rd exopods each with four spines and one plumose seta; 4th exopod with two spines and one plumose seta. Fifth legs of the usual pattern, basal expansion with two setae on each side; distal segment with three setae. Caudal rami little more than twice as long as wide, with three unequal setae.

Male. Unknown.

This species differs from all other species so far described in the presence of 2-segmented exopods in legs 1–4.

Genus Remanea Klie, 1929

This genus was described by Klie to receive a new copepod obtained in Kiel Bay. While it differs from *Paramesochra* and *Leptopsyllus* in the presence of a 3-segmented 1st exopod and the 2-segmented exopod of the 2nd antenna, it resembles many species of *Paramesochra* in its shape and in the 5th legs which are fused for part of their length. It appears to me to be a related genus.

Remanea arenicola Klie, 1929.

Occurrence. Fintry Bay, Isle of Cumbrae, Firth of Clyde; washed from fairly coarse sand near low-water mark.

Distribution. Kiel Bay, in coarse sand.

Several specimens of this copepod were taken in 1935 from the relatively coarse sand of Fintry Bay on the west shore of the Cumbrae, exposed to rough weather. These specimens are very slightly larger than those found by Klie (female 0·38 mm.), but that is the only difference.

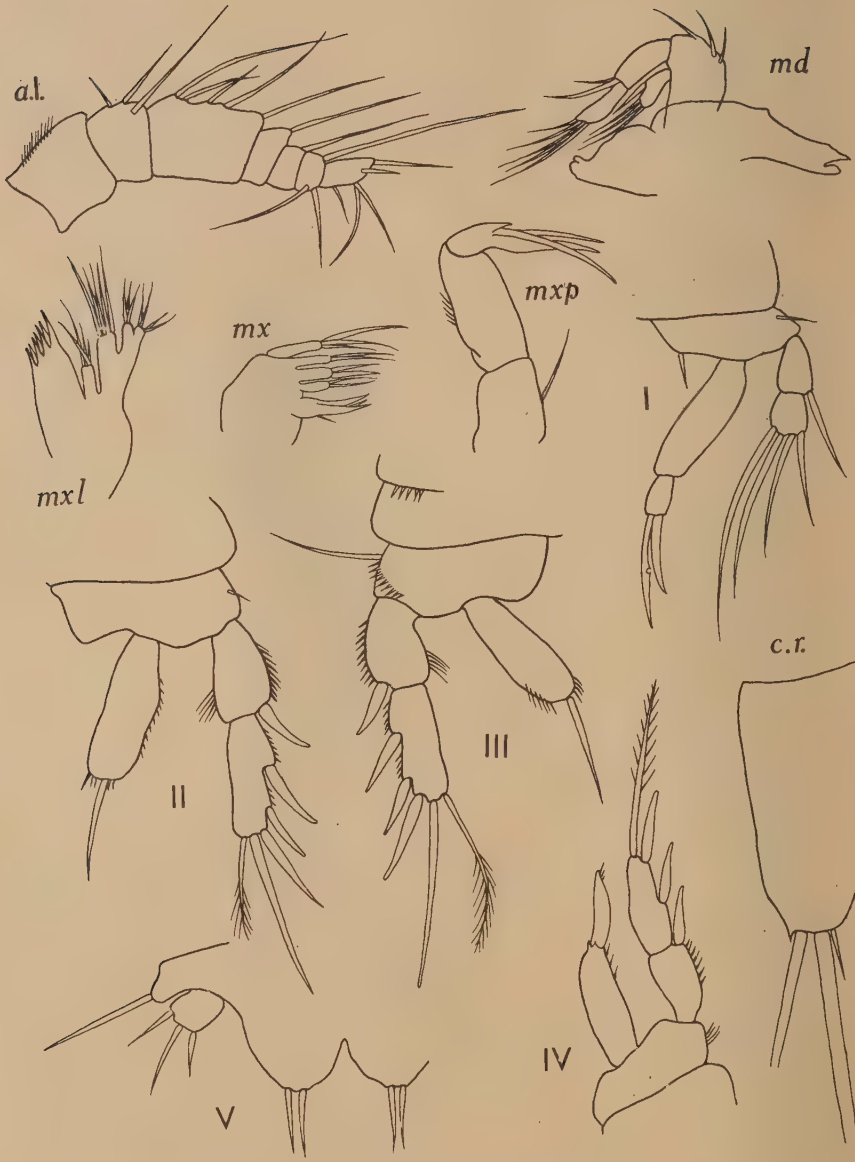

a.l.
md
mxl
mx
mxp
I
II
III
IV
V
c.r.

Fig. 7. *Paramesochra laurentica* n.sp. Female only.
All figures drawn to the same scale.

REFERENCES

Klie, W., 1929. Die Copepoda Harpacticoida der südlichen und westlichen Ostsee mit besonderer Berücksichtigung der Sandfauna der Kieler Bucht. *Zool. Jahrb.*, Bd. 57, pp. 329–86.

—— 1934. Die Harpacticoiden des Küstengrundwassers bei Schilksee (Kieler Förde). *Schr. Naturwiss. Ver. Schleswig-Holstein*, Bd. xx, pp. 409–21.

Kunz, H., 1937. Neue Harpacticoiden (*Crustacea Copepoda*) von Helgoland. *Kieler Meeresf.*, Bd. I, pp. 352–8.

—— 1938. Die Sandbewohnenden Copepoden von Helgoland. I. *Kieler Meeresf.*, Bd. II, pp. 223–54.

Lang, K., 1936. Die während der Schwedischen Expedition nach Spitzbergen 1898 und nach Grönland 1899 eingesammelten Harpacticiden. *Kungl. Svenska Vetensk. Handl.*, 3rd ser., Vol. xv, No. 4, pp. 1–55.

Monard, A., 1935. Étude sur la faune des Harpacticoïdes marins de Roscoff. *Trav. Stat. Biol. Roscoff*, Fasc. 13, pp. 1–90.

Nicholls, A. G., 1935. Copepods from the interstitial fauna of a sandy beach. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 379–406.

Scott, T., 1892. Additions to the fauna of the Firth of Forth. IV. *10th Ann. Rep. Fish. Bd. Scot.*, Pt. III, pp. 244–72.

—— 1894. Additions to the fauna of the Firth of Forth. VI. *12th Ann. Rep. Fish. Bd. Scot.*, Pt. III, pp. 231–71.

Scott, T. & Scott, A., 1895*a*. On some new and rare Crustacea from Scotland. *Ann. Mag. Nat. Hist.*, Ser. 6, Vol. xv, pp. 50–9.

—— —— 1895*b*. On some new and rare species of Copepoda from Scotland. *Ann. Scot. Nat. Hist.*, pp. 28–35.

Thompson, I. C. & Scott, A., 1900. Some recent additions to the Copepoda of Liverpool Bay. *Trans. L'pool. Biol. Soc.*, Vol. xiv, pp. 139–44.

Wilson, C. B., 1932. The copepods of the Woods Hole region, Massachusetts. *U.S. Nat. Mus.*, Bull. 158.

THE HYDROID OF THE MEDUSA *DIPURENA HALTERATA* (FORBES)

By W. J. Rees, M.Sc.

Research Assistant at the Plymouth Laboratory

(Text-figs. 1–3)

Although the medusa *Dipurena halterata* (Forbes, 1846) is well known, and has been figured by a number of authors (e.g. Forbes, 1848; Browne, 1897), the hydroid of this peculiar species has remained unknown. This medusa is rather scarce at Plymouth (Russell, 1938). On May 3 1938 I had the good fortune to find at Plymouth a small hydroid of the *Syncoryne* type which later liberated young medusae, and these proved to be young specimens of *Dipurena halterata*.

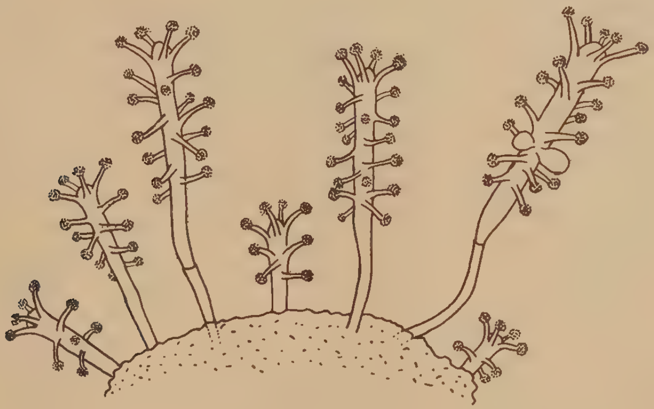


Fig. 1. Portion of colony of *Dipurena halterata*; Plymouth, 4. v. 38.

The hydroid was found growing on and in a sponge, *Chalina montagui* (Bowerbank), attached to a piece of *Lepralia foliacea* (Ellis & Solander), dredged near the Mewstone. Another piece of sponge from the same locality carried a young colony of the hydroid.

The Hydroid. The colony was small, with a total height rarely exceeding 2·5 mm. (Fig. 1). At first sight the polyps appeared to be very similar to those of *Zanclea implexa* (Alder). The polyps had the brownish or reddish colour common in species of *Syncoryne*. There were no stolons on the surface of the sponge, but there were many branching stolons deeply buried in the substance of the sponge. In the fully developed polyps the stems, covered by a thin non-annulated perisarc, reached a height of 0·5–0·8 mm. above the surface of the sponge. Young polyps on the surface were sessile with no visible hydrocaulus. Hand sections kindly prepared by Mr L. R. Crawshay, who identified the sponge, revealed that the young hydranths began their development deep down in the substance of the sponge and later forced their way to the surface. These buried rudimentary polyps possessed short tentacles with capitate heads which later, on reaching the surface, developed into typical tentacles. The sponge itself appeared to be in an emaciated condition, but whether this was due to the presence of the hydroid was impossible to determine because of the lack of adequate material. A detailed study of this association might prove well worth while.

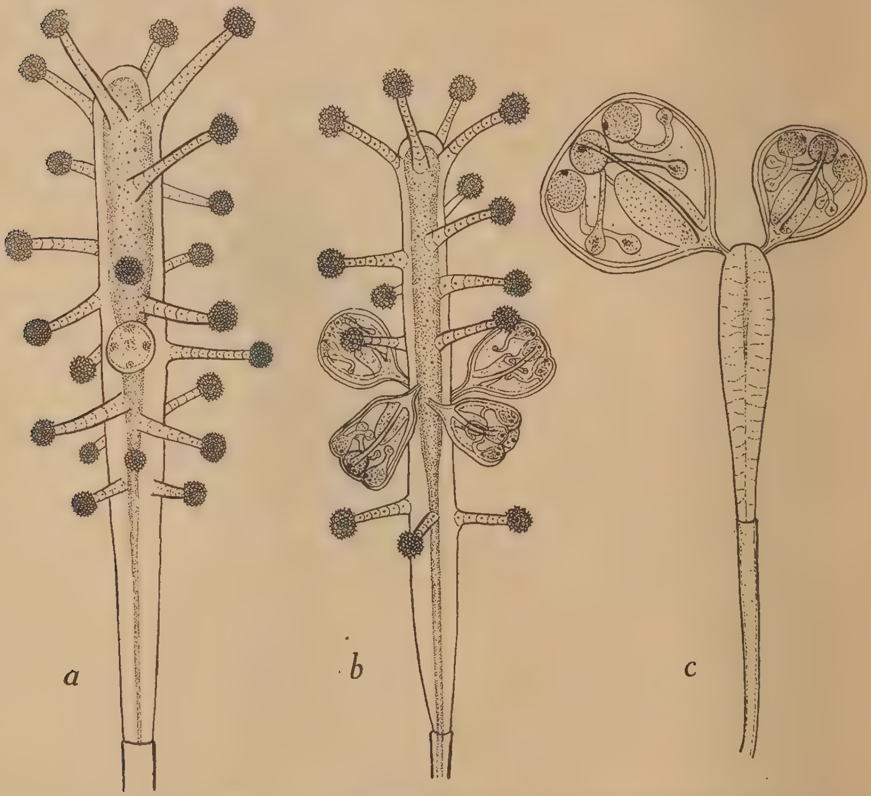


Fig. 2. *Dipurena halterata*; *a*, fully developed hydranth with a young medusa bud, 5. v. 38; *b*, hydranth with four medusa buds, 12. v. 38; *c*, hydranth reduced to a blastostyle, 18. v. 38; all from Plymouth.

The fully developed hydranths were 1·0–1·7 mm. in length with a diameter of 0·14–0·15 mm. The tentacles were all capitate, 17–24 in number. The distal end of the hydranths had four or five tentacles more or less in a whorl around the mouth. The other tentacles were irregularly scattered over the anterior and middle parts of the hydranth while the posterior part carried no tentacles (Fig. 2*a*). These tentacles were longer than the diameter of the hydranth and had capitate heads 0·06–0·08 mm. in diameter.

Medusa buds were borne on the hydranth a little behind the middle region of the body (Fig. 2*b*). Fully developed buds were covered by a thin transparent perisarc and were 0·40–0·45 mm. in diameter. A single hydranth had one to three medusa buds on it at the same time. These medusa-bearing hydranths usually became reduced to blastostyles devoid of tentacles (Fig. 2*c*).

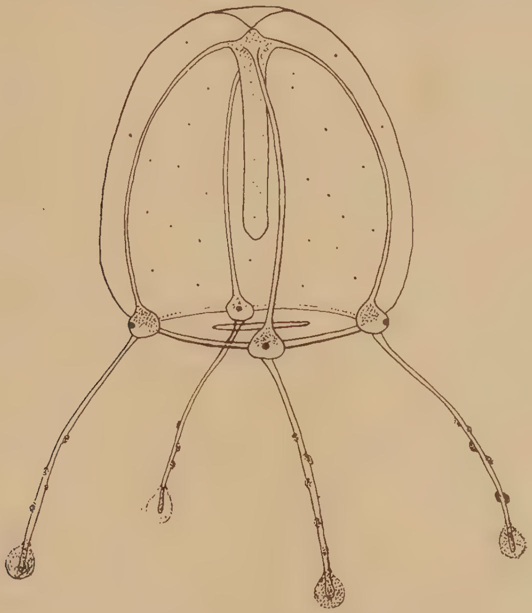


Fig. 3. Newly liberated medusa of *Dipurena halterata* obtained from the hydroid; Plymouth, 6. v. 38.

THE MEDUSA. The newly liberated medusa was bell-shaped, a little higher than wide, with a height of 1·5–1·6 mm. and a diameter of 1·3–1·4 mm. (Fig. 3). The umbrella had a fairly thin jelly with a few scattered nematocysts on its exumbrellar surface. The velum was broad. The stomach was cylindrical, reaching to about two-thirds of the height of the subumbrellar cavity. The mouth was simple without lips. The radial canals and ring canal were very narrow. There were four perradial tentacles arising from distinct bulbs each with a prominent black ocellus. The ends of the tentacles were swollen to form distinct knobs armed with batteries of nematocysts. The distal half of the tentacles also carried small irregularly placed batteries of nematocysts. The colour of the manubrium was a pale green, while the tentacle bulbs and the endoderm of the capitate ends of the tentacles were brick red in colour. At this stage there was no green colour in the tentacle bulbs, it appeared later, however, in the specimens which I reared.

One reared specimen reached a bell height of 2·8 mm. and a diameter of 2·5 mm. At this stage the linear swellings on the radial canals had developed. These were regarded by Forbes (1848) as ovaries, but it has since been shown by Haeckel (1879) and Browne (1897) that the gonads develop on the manubrium. The exact nature of these swellings is still unknown. Similar swellings have been observed by Russell & Rees (1936) on the radial canals of *Zanclea*. The terminal knobs on the tentacles were now much bigger than in the newly liberated medusa and had a diameter of 0·16–0·22 mm. The irregularly placed batteries of nematocysts of the young medusa were now developing into complete rings of nematocysts. The best developed tentacle possessed three complete rings and one incomplete ring of nematocysts as well as the terminal knob.

During July and August 1938 I collected many specimens of *Dipurena halterata* in various stages of development from the plankton at Valentia Harbour, Co. Kerry. A comparison of the young stages from Valentia with those reared from the hydroid at Plymouth confirms earlier observations made in this paper that the hydroid and its young medusa are stages in the life history of *D. halterata*.

Although the hydroid is of the *Syncoryne* type it cannot be referred to *Syncoryne* because the characters of the medusa alone are sufficient to warrant the generic distinction of the species from *Syncoryne*. It is therefore proposed to retain the name *Dipurena halterata* for both hydroid and medusa.

I am indebted to the Royal Society for a grant to cover my expenses at Valentia Island.

REFERENCES

Forbes, Edward, 1848. *A Monograph of the British Naked-eye Medusae*, pp. 1–104. Ray Society.

Browne, E. T., 1897. On British medusae. *Proc. Zool. Soc. London*, pp. 816–35.

Haeckel, Ernst, 1879. *Das System der Medusen*, pp. 1–672.

Russell, F. S., 1938. The Plymouth offshore medusa fauna. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 411–40.

Russell, F. S. & Rees, W. J., 1936. On rearing the hydroid *Zanclea implexa* (Alder) and its medusa *Zanclea gemmosa* McCrady, with a review of the genus *Zanclea*. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 107–29.

ON THE NEMATOCYSTS OF HYDROMEDUSAE. II

By F. S. Russell, F.R.S.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–4)

In a previous publication (Russell, 1938) I described the nematocysts in twenty species of Hydromedusae. The present report gives observations on five more species among which are three species of *Aequorea*. Among the medusae there is perhaps no genus in which the identity of the different species has been so confused as that of *Aequorea*. This genus is characterized by a large number of radial canals, and the specific distinctions are chiefly based on the number of these canals and the ratio that this number bears to the number of marginal tentacles. But in any one species neither are constant in number, and indeed both may show considerable variation in either direction. This is perhaps only to be expected since the character is of a meristic nature and must be dependent upon the rate of growth of the individual and the size to which it grows under different conditions. The type of the genus as selected by Haeckel (1879) is *A. forskalea* Péron & Lesueur. This name was given by Péron & Lesueur (1809) to a medusa described and figured by Forskål (1775, p. 110 and 1776, pl. xxxii) as *Medusa aequorea*. Some authors (e.g. Bigelow, 1913, p. 38) have retained the specific name *aequorea*, but this name cannot be kept since it had been used previously both by Linnaeus* and by Löfling (1858) for species which were inadequately described. Forskål's drawing is excellent and leaves no doubt as to which species he had. The usual number of radial canals is about 60–80 (cf. Claus, 1883; and Fraser, 1916). In his description, however, Forskål says that there are 129 canals, but he also states that these are paired, and we are probably right in assuming, as Claus (1883) did, that he was referring to the lamellae of the gonads and that the radial canals were really half this number. The medusa figured by Forskål has 104 radial canals and 105 tentacles. This is slightly more than is usual, but occasional large specimens may be found with 90–100 or slightly more canals. The species was excellently described in full detail and in all its stages by Claus (1883) as *A. forskalea*, and this is an additional argument for keeping that name.

A. forskalea forms an excellent type for the genus, for its characters can be regarded as forming a central point from which other species depart in different directions. Ideally it is a species in which the numbers of radial canals, mouth lips, and marginal tentacles are equal. But owing to slightly different rates of growth and development of the three characters this degree of perfection is rarely exactly attained. Thus the tentacles may be fewer or more than the radial canals, but they are hardly ever less than half or more than twice the number of canals. The tentacles also do not always appear on the umbrella margin opposite the radial canals, probably because, if the tentacle happens to be the first of the two to develop, the corresponding radial canal does not always grow along the exact line necessary to reach the ring canal opposite the tentacle.

---

* The description given by Linnaeus in *Systema naturae*, 10th edition, 1758, p. 659, refers to Loefling's medusa. It may be questioned whether this medusa belongs to the same genus. I have not seen Loefling's original description, but Péron & Lesueur (1809) give for it "point de bras", i.e. "no mouth lips"; this probably fits the genus *Aequorea* better than any other.

Bearing these facts in mind the identification of this species becomes much easier, and I have as a result found little difficulty in distinguishing it from two other species which occur off Plymouth. These are *A. vitrina* Gosse, whose number of tentacles far exceeds that of the radial canals, and *A. pensilis* (Modeer), whose number of radial canals far exceeds that of the tentacles.

An examination of the nematocysts of these three species has confirmed their separation.

The other two species whose nematocysts are described in this paper are the siphonophores *Agalma elegans* (M. Sars) and *Velella velella* (L.). The nematocysts of *Aequorea forskalea* and *A. vitrina* were examined on medusae preserved in formalin and sea water. For the other three species observations were made on fresh material.

LEPTOMEDUSAE

Aequorea forskalea Péron & Lesueur

I am indebted to Mr P. G. Corbin for a collection of many *A. forskalea* taken in the mouth of the English Channel in July 1937. These specimens were between 45 and 100 mm. in diameter; they had 64–99 radial canals and 51–79 tentacles. The ratio of the diameter of the stomach to that of the umbrella varied approximately from 1 : 1·8 to 1 : 2·4.

The nematocysts, both in the marginal tentacles and the mouth lips were of two kinds: basitrichous haplonemes* and atrichous haplonemes (Fig. 1 *a–c*).

Basitriches: 12–18 × 2·5–4 μ undischarged.

Atriches: 17–34 × 7–17 μ undischarged.

Both types of nematocyst showed considerable variation in size from one specimen to another. This was especially noticeable in the large oval atriches, which tended to fall into two size groups 17–22 and 26–34 μ long, both sizes being present in a single specimen, but only the smaller size occurring in the mouth lips.

My results thus differ from those of Weill (1934, p. 458) who states that basitriches are not present in the mouth lips. He gives the size of the basitriches as 15 μ long and that of the atriches as 15–20 μ.

---

* I cannot be sure whether these nematocysts, in this and the next two species of *Aequorea*, are basitrichous haplonemes or microbasic mastigophores (see Russell, 1938, p. 146).

Now that I have seen so many specimens of *A. forskalea* I think there can be little doubt that *A. forbesiana* of Gosse (1853) is the same species.

Aequorea vitrina Gosse

I have seen four specimens of *A. vitrina*, whose characters were as follows:

Diameter of umbrella mm.	Diameter of stomach mm.	No. of radial canals	No. of tentacles	No. of mouth lips
55	25	76	*ca.* 304	..
75	37	68	*ca.* 275	..
80	40	68	> 300	*ca.* 39
90	40	90	*ca.* 600	*ca.* 40

The nematocysts both in the marginal tentacles and in the mouth lips were of two kinds: basitrichous haplonemes and atrichous haplonemes (Fig. 1 *d*, *e*).

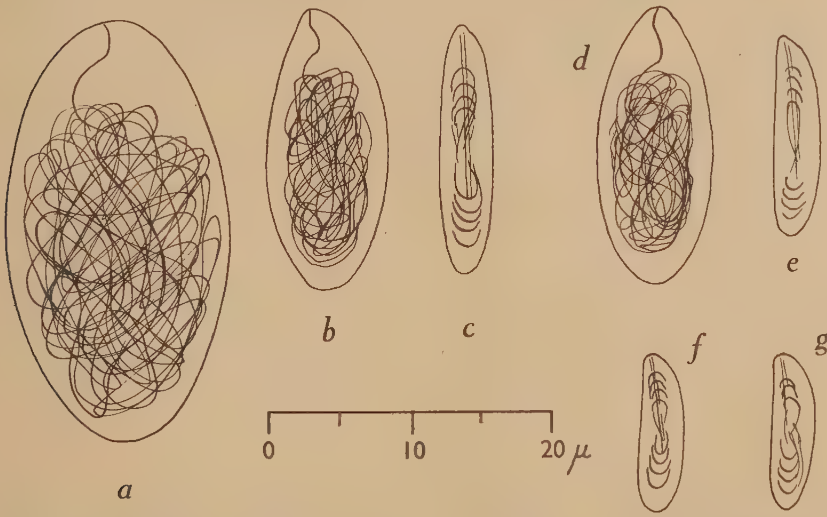


Fig. 1. *a–c*, *Aequorea forskalea*; *a*, *b*, atrichous haplonemes; *c*, basitrichous haplonemes; *d*, *e*, *A. vitrina*; *d*, atrichous haploneme; *e*, basitrichous haploneme; *f*, *A. pensilis*, basitrichous haploneme; *g*, ? *A. pensilis*, basitrichous haploneme. × *ca.* 2000.

Basitriches: 10–15 × 2·5–3 μ undischarged.

Atriches: 19–22 × 7·5–8·5 μ undischarged.

The very large atrichous haplonemes, characteristic of *A. forskalea* were absent.

The number of mouth lips, estimated on the basis of the number of transparent lines of large endodermal cells running down the stomach wall, appears to be usually in the neighbourhood of half or less than half the number of radial canals in *A. vitrina*, whereas in *A. forskalea* they are of more nearly the same number as the radial canals.

The specimens described by Hartlaub (1894) as *A. forskalea* are clearly *A. vitrina.*

Evans & Ashworth (1909) recorded a number of medusae from the Firth of Forth, which were identified by E. T. Browne as *A. norvegica* Browne. I have found one of these specimens in Mr Browne's collection. Its nematocysts were of the same types and approximately the same size as those of *A. vitrina.*

Basitriches: 12–13 × 3 μ undischarged.

Atriches: 18–20 × 7·5–8 μ undischarged.

The numbers of mouth lips both in the medusae described by Evans & Ashworth and in the type specimen of *A. norvegica* described by Browne (1903) also agree with those of *A. vitrina.* I am therefore inclined to agree with the suggestion made by Kramp (1933) that *A. norvegica* and *A. vitrina* are the same species. There is, however, an indication that the medusa does not grow to so large a size in these waters as it does farther north.

A. vitrina evidently comes very close to *A. coerulescens* (Brandt) as described by Bigelow (1909). In fact if it were not for the deep bluish black pigmentation in the tentacle bulbs, which appears to be so characteristic of *A. coerulescens*, there does not seem to be any character by which they can be distinguished. Bigelow's photograph of that species (1909, pl. 4, fig. 4) might well be a typical *A. vitrina.* An examination of the nematocysts of *A. coerulescens* might be helpful.

On the American side of the Atlantic *A. vitrina* appears to be represented by *A. albida* A. Agassiz.

Both *A. forskalea* and *A. pensilis* are present in the Atlantic and the Pacific, and it seems reasonable to suppose that eventually *A. vitrina* may be shown to have a similar distribution by regarding *A. coerulescens* and *A. albida* as geographical races. We need, however, more detailed observations on the numerical characters of these species.

Aequorea pensilis (Modeer)

In September 1938 a number of medusae were collected off Plymouth which are undoubtedly *A. pensilis.* The nematocysts, both in the marginal tentacles and in the mouth lips, were only of one kind, basitrichous haplonemes (Fig. 1*f*).

Basitriches: 9–13 × 2·5–3 μ undischarged.

The medusae were thus immediately distinguishable from the two preceding species of *Aequorea* by the absence of large oval atrichous haplonemes.

The occurrence of *A. pensilis* off Plymouth was somewhat unexpected and it is necessary to discuss these specimens in some detail. Full details of the numerical characters are given in Table I. It will be seen that these characters agree well with those in the table drawn up by Bigelow (1919, p. 312).

Bigelow gives the ratio of radial canals to tentacles as between 10 : 1 and 12 : 1 for specimens of 60 mm. diameter and less. The Plymouth specimens, over a much larger range of numbers, show a ratio of 3·5 : 1 to 13 : 1. It is, however, to be observed that this ratio changes with the size of the medusa. In specimens under 40 mm. in diameter it varies between 8 : 1 and 13 : 1. Above this size the number of tentacles increases owing to the development of tentacles on some of the marginal bulbs. The ratio of the stomach diameter to that of the umbrella varies between 1 : 1·3 and 1 : 2·0, thus agreeing closely with the corresponding ratios of 1 : 1·4 to 1 : 2·0 derived from Bigelow's table. In all specimens the central mass of jelly was very thick, and in the form of a plano-convex lens, and anastomosis of the radial canals was frequent. The gonads were yellowish green overlain by bluish grey pigment: the green colouration disappeared after preservation.

TABLE I. *AEQUOREA PENSILIS* CAUGHT OFF PLYMOUTH, SEPTEMBER 1938

Diameter of umbrella mm.	No. of radial canals	No. of tentacles	Ratio of radial canals : tentacles	Diameter of stomach mm.	Ratio of diameter of stomach : umbrella
16	129	11	13 : 1	10	1 : 1·6
18	124	10	12 : 1	10	1 : 1·8
20	>117	13	..	15	1 : 1·3
20	128	16	8 : 1	15	1 : 1·3
20	122	11	11 : 1	13	1 : 1·5
22	137	12	11 : 1	14	1 : 1·6
22	121	12	10 : 1	15	1 : 1·5
25	127	12	11 : 1	17	1 : 1·5
27	>111	15	..	16	1 : 1·7
29	>126	16	..	18	1 : 1·6
30	>118	>16	..	18	1 : 1·7
30	146	13	11 : 1	16	1 : 1·9
30	139	15	9 : 1	17	1 : 1·8
30	130	12	11 : 1	15	1 : 2·0
32	125	15	8 : 1	18	1 : 1·8
35	127	16	8 : 1	19	1 : 1·8
35	148	15	10 : 1	25	1 : 1·4
37	146	11	13 : 1	19	1 : 1·9
37	123	>14	..	20	1 : 1·9
40	151	16	9 : 1	20	1 : 2·0
45	140	..	..	24	1 : 1·9
45	166	17	10 : 1	27	1 : 1·7
45	154	22	7 : 1	30	1 : 1·5
50	138	24	6 : 1	28	1 : 1·8
55	127	22	6 : 1	30	1 : 1·8
60	126	>21	..	30	1 : 2·0
60	140	34	4 : 1	38	1 : 1·6
60	144	41*	3·5 : 1	37	1 : 1·6
60	129	24	5 : 1	..	..
65	138	22	6 : 1	40	1 : 1·6
80	*ca.* 175†	..	..	55	1 : 1·5

* 18 large. † 85–90 in half—remainder damaged.

While in the above characters the specimens agree with *A. pensilis*, the structure of the tentacle bases is exactly like that of *A. macrodactyla* (Brandt); they are conical and laterally expanded, and clasp the umbrella margin and have a slight median spur (Fig. 2*c*, *d*). The median spur is prolonged downwards over the abaxial surface of the tentacle bulb as a median ridge. But the true condition of spur and ridge is only seen when the specimens are perfectly preserved. In many specimens the tentacle bulbs had become distorted and merely appeared as rather large laterally expanded swellings as has been described by various authors for *A. pensilis*. The tentacles are irregularly distributed round the umbrella margin. The number of marginal warts between adjacent tentacles is variable; usually there are about seven to nine. The marginal vesicles are extremely numerous and may exceed forty between two adjacent tentacles; each contains 2–5 concretions.

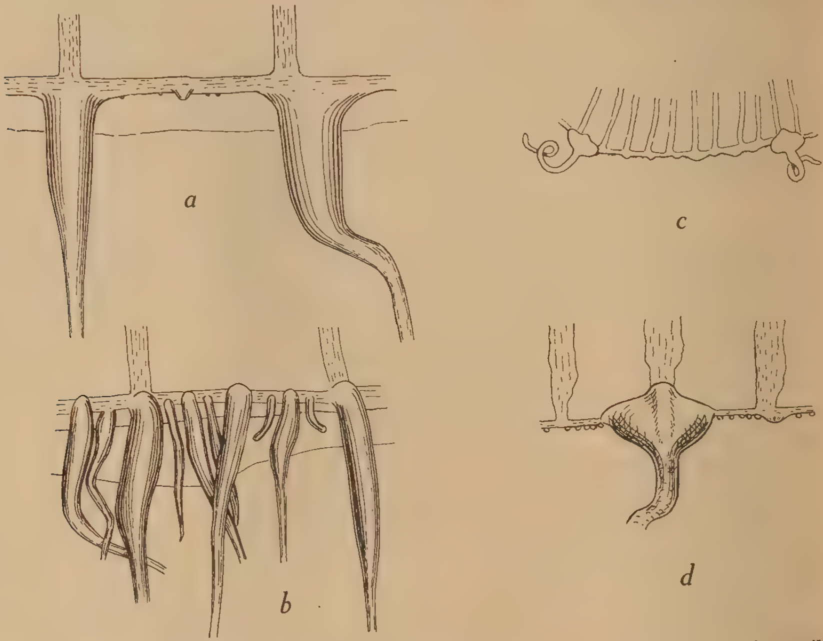


Fig. 2. Portions of umbrella margin of: *a*, *Aequorea forskalea*; *b*, *A. vitrina*; *c*, *d*, *A. pensilis*. (*a*, *b*, and *d* approximately to same scale; *c*, less enlarged.)

In many specimens it was impossible to find any excretory pores or papillae; in some, small slits without papillae could be found, while in others the papillae were quite distinct. The above three conditions might be found in the same specimen.

The Plymouth specimens thus appear to combine the characters of the two species *A. pensilis* and *A. macrodactyla*, except in so far as the number of radial canals is concerned; for *A. macrodactyla* is generally considered to have far fewer radial canals. Among the Plymouth medusae there was, however, one specimen (not included in Table I) which had only 63 radial canals. It was 27 mm. in diameter and had ten tentacles; the diameter of the stomach was 13 mm. In all other respects it was identical with the other specimens, and had the same single type of nematocyst. The occurrence of this one specimen among the others raises the question whether at times *A. pensilis* may have only half the normal number of radial canals and whether therefore *A. pensilis* and *A. macrodactyla* are really separate species. I will return to this later.

A. pensilis has not been recorded from the North Atlantic before. It is possible that the specimen so well figured by Forskål (1776) came from the Mediterranean, but he makes no mention of its origin and it may just as well have come from the Red Sea. But a search in the literature shows the occurrence of medusae which are probably *A. pensilis* recorded under other names.

The medusae referred to by Claus (1883, p. 80) as *A. discus* are most probably *A. pensilis*. Claus, who had seen so many typical *A. forskalea*, did not hesitate to regard this as a distinct species on account of its disproportionate number of radial canals. A summary of Claus's table for the characters of *A. discus* is given in Table II.

TABLE II

Diameter of umbrella mm.	No. of radial canals	No. of tentacles
7–8	59	8
12	95	8
15	112	8
20	94	16
30	93	16+

Browne (1897) describes six specimens from Valencia under the name of *forskalea*. While the largest of these is clearly *A. forskalea*, being 160 mm. in diameter and having 88 radial canals and 56 tentacles, the remaining five are just as clearly *A. pensilis*. Table III gives a summary of Browne's observation on these specimens.

TABLE III

Diameter of umbrella mm.	Diameter of stomach mm.	No. of radial canals	No. of tentacles
25	13	140	7
30	..	114	8
55	26	145	16
60	33	180	28
135	55	153	43

I have found a specimen in Mr Browne's collection taken on the same date as those mentioned above and it agrees with the Plymouth specimens in having only one type of nematocyst.

There can thus be little doubt that *A. pensilis* is a fairly common and widespread medusa, and as such it might be expected to show variation from place to place. We now have quite a number of observations for comparison and in Fig. 3 I have plotted the numbers of tentacles against the numbers of radial canals for most of the specimens recorded in the literature. These include the following specimens: those listed by Bigelow (1919, pp. 312, 314) as *A. pensilis** and *A. macrodactyla*; those recorded by Vanhöffen (1911, p. 232) as *Mesonema coelum pensile*; the Plymouth specimens recorded in this paper; and those recorded as *Aequorea discus* by Claus (1883, p. 80) and as *Polycanna forskalea* by Browne (1897, p. 829). The figure shows that there is a tendency towards two distinct groupings into *Aequorea macrodactyla* and *A. pensilis*. Yet this distinction does not seem to be sufficiently clear cut to warrant their separation into two species. It is preferable to regard them all as belonging to one species, *A. pensilis*, with a variety, *macrodactyla*, in which only half the full number of radial canals is developed. The occurrence of only one specimen of the latter type among the many specimens caught off Plymouth would seem to favour this view. It is possible that in some localities one or the other variety might predominate. This splitting of the one species into two varieties is also more convenient, since, with increasing observations, specimens are sure to be found on the border line between the two, whose identity would be uncertain if the two species were kept distinct.

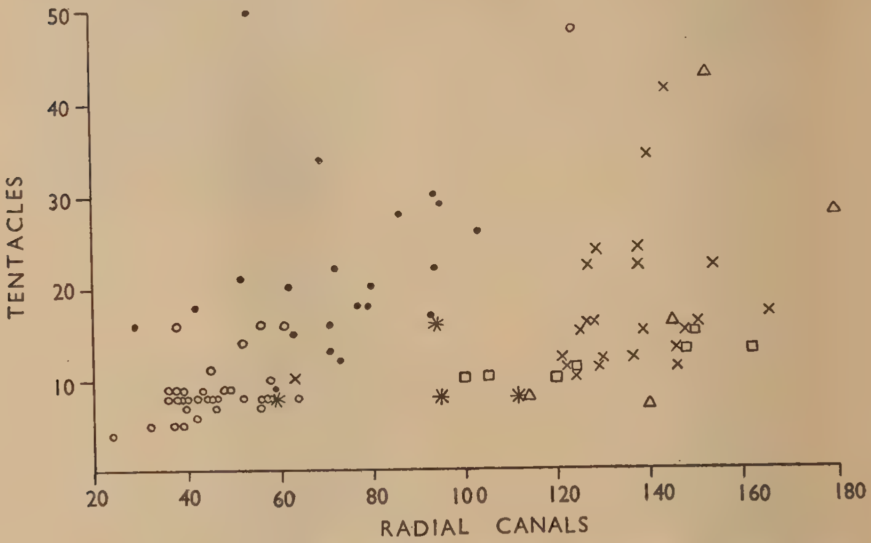


Fig. 3. Ratio of number of marginal tentacles to number of radial canals of *Aequorea pensilis* from the following sources. □, *A. pensilis*, and ●, *A. macrodactyla* from Bigelow (1919, pp. 312, 314); ○, *Mesonema coelum pensile* of Vanhöffen (1911, p. 232); ×, *A. pensilis* from Plymouth, recorded in this paper; *, *A. discus* of Claus (1883, p. 80); and △, *Polycanna forskalea* of Browne (1897, p. 829).

Mention should be made here of another specimen of *Aequorea*. On

---

* Excluding the two of Maas (1905) with *ca.* 200 and 250 canals.

October 4 1932 the weekly oblique haul with the 2 m. ring trawl contained fragments of a large medusa. Fragments of about five-sixths of this specimen were present and it must have been about 180 mm. in diameter. There were 114 radial canals, making a probable total of about 140, and the tentacles were about two-thirds the number of radial canals and very irregularly distributed. The gonads were bluish grey in colour. The tentacle bulbs appeared more like those of *A. forskalea*, but they had become very much squashed in preservation. On examining the nematocysts, it was found that both in the tentacles and mouth lips only one type was present, namely basitrichous haplonemes.

Basitriches: 10–11 × 2·5–3 μ undischarged (Fig. 1*g*).

The large atrichous haplonemes so typical of *A. forskalea* were absent. I hesitate to identify this medusa for certain, but from the number of radial canals and the type of nematocyst it seems possible that it may have been a very fully developed *A. pensilis* in which the number of tentacles has increased considerably. The specimen appears to agree with that described by Forbes (1851) from the Minch as *A. forskalea*. His specimen, *ca.* 130 mm. (5 in.) in diameter, had 136 radial canals and *ca.* 68 large tentacles, with 68 small tentacles and 136 marginal bulbs.

ON THE IDENTIFICATION OF THE THREE PLYMOUTH SPECIES OF *AEQUOREA*

The distinguishing characters of the three species, *A. forskalea*, *A. vitrina*, and *A. pensilis* including var. *macrodactyla*, in their adult stages, can now be defined as follows.

	forskalea	*vitrina*	*pensilis*
No. of radial canals	Usually 60–80 rarely exceeding 100	60–90	*ca.* 120–180 or half this number
No. of tentacles	*ca.* 40–85, usually approximating to number of radial canals, rarely less than half or more than twice	*ca.* 300 or more; always exceeding number of radial canals by more than three times	Usually less than, often much less than, one-third of the number of radial canals
Tentacle bases	Elongated and conical (Fig. 2*a*)	Elongated, and slightly laterally compressed (Fig. 2*b*)	Conical, laterally expanded, often with median spur (Fig. 2*c*, *d*)
Mouth lips	Approximating to number of radial canals*	Usually about half the number of radial canals	Approximating to number of radial canals†
Umbrella diameter / stomach diameter	*ca.* 1·8–2·4	*ca.* 1·8–3·0	*ca.* 1·3–2·0
Nematocysts	Two kinds	Two kinds	One kind

* Fraser (1916) states that the mouth lips are never more than half the number of radial canals in specimens from Departure Bay in the Pacific. This may be a geographical variation.

† Maas (1905) gives figures in the neighbourhood of half the number of radial canals: his drawing (pl. viii, fig. 54), however, shows approximately equal numbers.

The ratio of the number of tentacles to the number of radial canals is also a sure guide for the identification of the young stages of the three species. Some difficulty may, however, arise in separating the young of the *macrodactyla* variety of *A. pensilis* from the young of *A. forskalea*. But herein lies the value of a study of the nematocysts, for it is only necessary to crush a tentacle under a cover glass, or take a piece of mouth lip, and examination under the microscope with a $\frac{1}{6}$ in. objective will disclose at once the presence or absence of the conspicuous atrichous haplonemes characteristic of *A. forskalea*. An additional diagnostic character for young stages appears to lie in the number of marginal vesicles. In *A. forskalea* there are only one or two marginal vesicles between adjacent marginal bulbs and tentacles, whereas in *A. pensilis* they are much more numerous.

Of the three species *A. vitrina* appears to be the most northerly in its distribution and *A. pensilis* is perhaps most confined to warm water.

It is not without interest to note here that, among the Leptomedusae that I have examined so far, I have only found one other species besides *A. pensilis* in which I could see no atrichous haplonemes. This was *Phialella cymbaloides*. It suggests the possibility that *Aequorea pensilis* and the other two species of *Aequorea* may have evolved separately.

SIPHONOPHORA

Agalma elegans (M. Sars)

Although the identity and synonymy of *A. elegans* (M. Sars) is well known it will be as well to state here that the species examined was that with the tricornuate tentillae, since Sars described two species under the one name.

There were four kinds of nematocysts. Large microbasic mastigophores and anisorhize homotrichous haplonemes, in the batteries of the tentillae; desmonemes in the two terminal filaments of a tentilla; and microbasic euryteles situated at the ends of the tentacles and in two small groups on either side of the velar openings of the nectophores (Fig. 4*a*–*h*).

Mastigophores: 185–205 × 25–28 μ undischarged.

The thread was beset along its whole length with three rows of stout barbs.

The barbs appear to be set in three parallel longitudinal rows and not spirally (cf. Schneider, 1900, p. 101).

Anisorhize: up to *ca.* 75 × 6–7 μ undischarged.

The smallest nematocysts of this type were *ca.* 22 × 4 μ.

Desmonemes: 6–7 × 6 μ undischarged.

Euryteles: 90–105 × 30–35 μ undischarged; *ca.* 70–23 μ discharged.

These large euryteles had three basal stylets similar to those of stenoteles.

In addition to the above nematocysts there were large numbers of "anacrophores" in the terminal filaments and distal ends of the spiral nematocyst bands. These ranged in size from 7 × 2 to 20 × 5 μ undischarged. In a previous publication (Russell, 1938) I suggested that these may be stages in the develop-

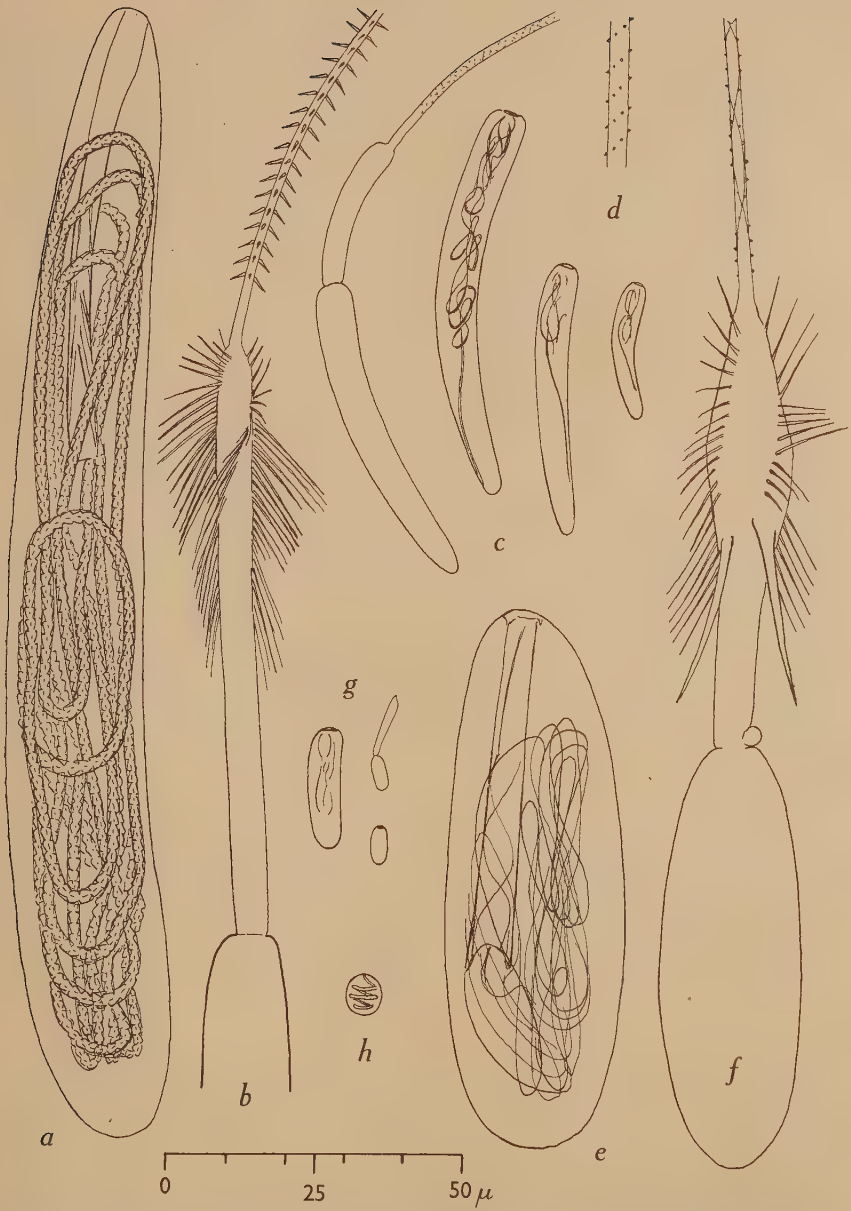


Fig. 4. *Agalma elegans*: *a*, *b*, microbasic mastigophore; *c*, anisorhize haplonemes of different sizes, with enlarged portion of thread, *d*; *e*, *f*, eurytele; *g*, "anacrophores"; *h*, desmoneme. × *ca*. 850.

ment of the desmonemes and anisorhize haplonemes. After seeing the nematocysts of *Agalma elegans* I am inclined to modify this suggestion and say that they are anisorhize haplonemes in an arrested state of development. Among the anisorhize haplonemes a complete range in size may be found in any one battery from the smallest "anacrophore" upwards. The "anacrophores" up to a length of about 20 μ are straight with rounded ends, while the smallest anisorhize haplonemes down to a length of about 27 μ are tending towards this shape. It is also noticeable that the smaller the anisorhize the shorter is its thread. There does, however, usually appear to be a break in the series between about 20 and 27 μ.

Velella velella (L.)

In October 1938 a small specimen of *Velella*, *ca.* 15 mm. long, was caught in the plankton. There were two kinds of nematocysts: stenoteles and atrichous haplonemes.

Stenoteles: these were of two sizes, 18–21 × 14–16 μ and 13–15 × 10–11 μ undischarged.

Atriches: 8–9 × 4·5 μ undischarged.

The specimen when examined was in a very decomposed condition and the armature of the discharged stenoteles always broke away and could not be made out in detail.

These nematocysts agree fairly closely with the sizes given by Weill (1934, p. 516) for specimens from Samoa preserved in alcohol in the British Museum. This is additional evidence in favour of the conclusion of Bigelow & Sears (1937) that the Atlantic and Pacific *Velella* are the same species.

SUMMARY

The nematocysts of the three species of Leptomedusae, *Aequorea forskalea*, *A. vitrina*, and *A. pensilis*, and of the two siphonophores *Agalma elegans* and *Velella velella* are described.

The specific characters of the three species of *Aequorea* are discussed and it is shown that *A. pensilis* is probably the same species as *A. macrodactyla*.

REFERENCES

BIGELOW, HENRY B., 1913. Medusae and Siphonophorae collected by the U.S. Fisheries Steamer "Albatross" in the North-western Pacific. *Proc. U.S. Nat. Mus.*, Vol. 44, No. 1946, pp. 1–119.

—— 1909. Reports on the scientific results of the expedition to the Eastern Tropical Pacific.... XVI. The medusae. *Mem. Mus. Comp. Zoöl. Harvard*, Vol. XXXVII, pp. 1–243.

—— 1919. Hydromedusae, siphonophores and ctenophores of the "Albatross" Philippine Expedition. *Bull. U.S. Nat. Mus.*, 100, Vol. 1, Pt. 3, pp. 279–362.

BIGELOW, HENRY B. & SEARS, MARY, 1937. Siphonophorae. *Rep. Danish Ocean. Exp.*, 1908–1910, Vol. II, Pt. 2, pp. 1–144.

BROWNE, EDWARD T., 1897. On British medusae. *Proc. Zool. Soc. London*, pp. 816–35.

—— 1903. Report on some medusae from Norway and Spitzbergen. *Bergens Mus. Aårb.*, No. 4, pp. 1–36.

CLAUS, CARL, 1883. *Untersuchungen über die Organisation und Entwicklung der Medusen.* 96 pp. Leipzig.

EVANS, WM. & ASHWORTH, J. H., 1909. Some medusae and ctenophores from the Firth of Forth. *Proc. Roy. Phys. Soc. Edinb.*, Vol. XVII, No. 6, pp. 300–11.

FORBES, EDWARD, 1851. On a species of *Aequorea* inhabiting the British Seas. *Proc. Zool. Soc. London*, Pt. XIX, pp. 272–5.

FORSKÅL, PETRUS, 1775. *Descriptiones animalium, avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskål. Post mortem auctoris edidit Carsten Niebuhr.* 164 pp. Hauniae.

—— 1776. *Icones rerum naturalium, quas in itinere orientali depingi curavit Petrus Forskål. Post mortem auctoris ad Regis mandatum aeri incisas edidit Carsten Niebuhr.* Pl. I–XLIII. Hauniae.

FRASER, C. MCLEAN, 1916. On the development of *Aequorea forskalea*. *Trans. Roy. Soc. Canada*, Ser. III, Vol. X, pp. 97–104.

GOSSE, PHILIP HENRY, 1853. *A Naturalist's Rambles on the Devonshire Coast.* John van Voorst, London, 451 pp.

HAECKEL, ERNST, 1879. *Das System der Medusen.* Jena.

HARTLAUB, CLEMENS, 1894. Die Coelenteraten Helgolands. *Wiss. Meeresuntersuch. Abt. Helgoland*, N.F., Bd. 1, Heft 1, IV, pp. 161–206.

KRAMP, P. L., 1933. *Nordisches Plankton*, Lief. 22, XII. Craspedote Medusen. 3 Teil. Leptomedusen, pp. 541–602.

LÖFLING, P., 1758. ...*Iter Hispanicum*.... 316 pp. Stockholm.

MAAS, OTTO, 1905. Die Craspedoten Medusen der Siboga-Expedition. *Siboga-Expeditie*, Vol. X, pp. 1–84.

PÉRON & LESUEUR, 1809. Histoire générale et particulière de tous les animaux qui composent la famille des Méduses. *Ann. Mus. Hist. Nat. Paris*, Tome XIV, pp. 312–66.

RUSSELL, F. S., 1938. On the nematocysts of Hydromedusae. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 145–65.

VANHÖFFEN, E., 1911. Die Anthomedusen und Leptomedusen der Deutschen Tiefsee-Expedition 1898–1899. *Wiss. Ergeb. Deutsch. Tiefsee-Exped. Valdivia* 1898–1899, Bd. XIX (1925), Heft 5, pp. 193–233.

WEILL, ROBERT, 1934. Contribution à l'étude des cnidaires et de leurs nématocystes. II. Valeur taxonomique du cnidome. *Trav. Stat. Zool. Wimereux*, Tome XI, pp. 349–701.

SEASONAL VARIATIONS IN THE FAT CONTENT OF THE FLOUNDER, *PLEURONECTES FLESUS* L.

By Douglas P. Wilson, M.Sc.
Naturalist at the Plymouth Laboratory

(Text-figs. 1–5)

CONTENTS

	PAGE
Introduction	361
Methods	361
Distribution of the adipose tissue	365
Immature flounders in the estuaries	367
Maturing and spawning flounders	369
Recovery of spent fish	371
The region of the superficial lateral muscle	372
Discussion	376
Summary	379
References	379

INTRODUCTION

In only a few fishes has any attempt been made to trace variations in the fat content from season to season and during the spawning period. Of the economically important herring, however, a great many seasonal fat analyses have been made, and more than one species of salmon has received attention from this point of view. So far as I am aware little has been done along similar lines for any of the bottom-dwelling flat fishes. When, therefore, there arose an opportunity of examining a plentiful supply of flounders, about which a good deal of other relevant information would be available, it was decided to concentrate on this species. The flounders in question were obtained by Mr P. H. T. Hartley during his investigations into the fisheries of the Tamar and Lynher estuaries. I am greatly indebted to him for his kindness in passing them on to me after he had weighed and measured them, noted the sex and maturity and removed the stomach of each fish. He subsequently supplied me with copies of his records which have proved invaluable.

METHODS

The fat content of a fish has sometimes been estimated approximately by visual judgement, as in assessing the quality of herrings by the amount of intestinal fat (ister) seen on opening the body cavity (Hjort, 1914; Bjerkan, 1917). Occasionally judgement has been made from frozen sections cut from selected regions of the body and stained by one of the fat stains. This was the method mainly employed by Greene in his important work on the storage of fat in the muscular tissue of the king salmon, *Oncorhynchus tschawytscha*. Some investigators have preferred the method of chemical analysis; in this connexion can be mentioned the work of Johnstone (1915, 1918) and of Bruce (1924) on the Manx herring. Johnstone partly confirmed his results by cutting paraffin sections of portions of the muscular tissue, thereby demonstrating variation in the quantity of adipose tissue present. As it is not usually the practice to analyse chemically the whole of one fish, and it is always difficult if not impractical to deal with large numbers in this way, the chemical method may be no more efficient in demonstrating seasonal or ontogenetic variations in fat content than is the histological method, provided that the species treated in the latter way is one which gives a clear picture of the fat when cut and stained. On the other hand, the histological method can demonstrate only fat which is in such a form as to be readily stainable, and it does not allow of the calculation of calorific values.

In the present work histological technique has been used throughout. It was early realized that the cutting, staining and mounting of frozen sections takes up too much time to allow a really large number of fish to be examined. A much simpler technique was therefore devised and one that gave a better fat picture for each fish. The method consisted of cutting a slice 1–2 cm. thick across the fish at its widest part midway between head and tail. Prior to cutting, the fish were hardened in 10 % formalin for at least several days. The slice was rinsed in 50 % alcohol and immersed in a solution of Scarlet Red (Sudan IV) in equal parts of 70 % alcohol and acetone contained in a tightly stoppered jar. After 20 min. to half-an-hour it was removed from the stain, washed in 50 % alcohol and then preserved in 5 % formalin. For the purpose of preservation formalin is not ideal and does not keep the sections in as good a condition as does glycerine. It will, however, keep them for a few weeks and sometimes months without much deterioration of the staining, and the slices can always be restained to some extent. When large numbers of such slices of fish have to be preserved glycerine is almost prohibitive on account of its cost. I have not noticed any difference in result between neutral and non-neutral formalin.

The method enabled fairly large samples of fish to be handled expeditiously, for a number of slices could be stained at one time. It was found unnecessary to take more than one slice from each fish. A series of slices down a fish all gave similar fat pictures.

The appearance of typical slices is illustrated in Fig. 1. Various regions would stain bright red and be large or small in area according to the amount of fat and adipose tissue present. In a fat fish areas roughly triangular in shape showed up distinctly among the muscles of the bordering fins. A bone, sliced across, generally showed more or less fat in and around it. The picture varied a little, of course, with the level of the cut, whether, for instance, it went

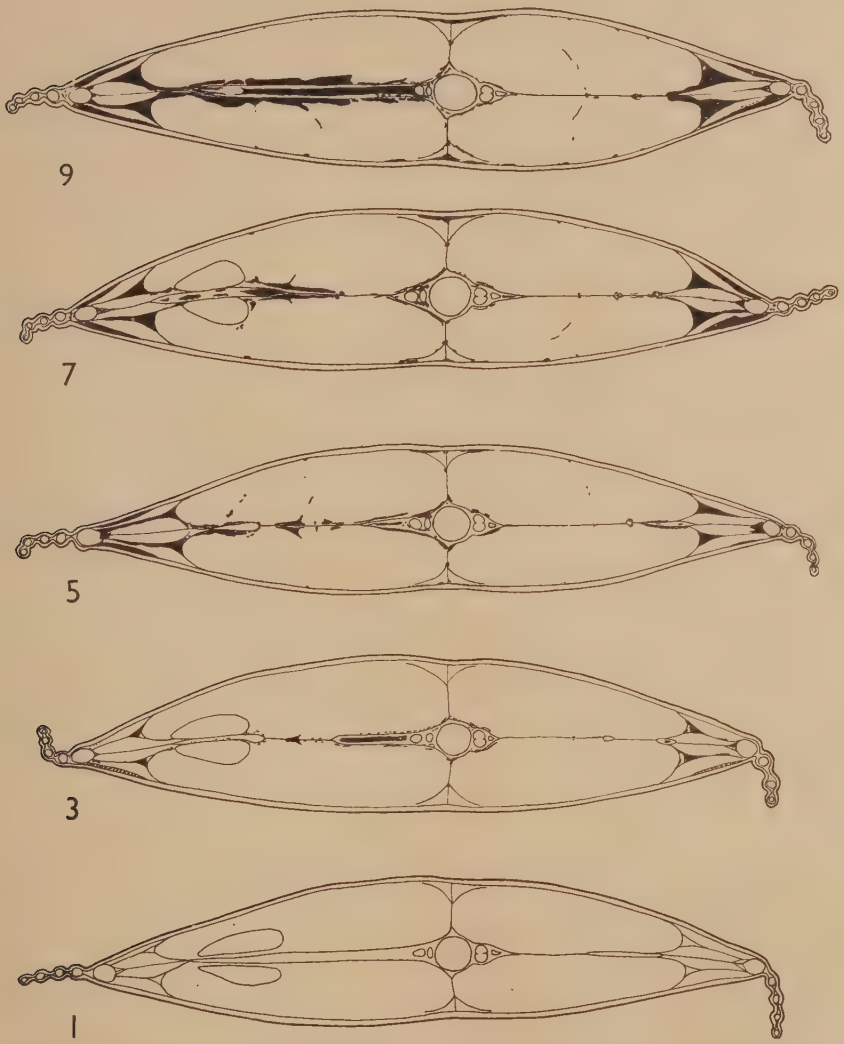


Fig. 1. Diagrammatic representations of transverse slices of the flounder midway between head and tail to show the relative amounts of fat in the five main arbitrary degrees as follows: 1, none; 3, little; 5, medium; 7, fat; 9, very fat. In this figure degrees 1, 3 and 7 are illustrated by female fish, 5 and 9 by male fish. The fish selected as typical for the purposes of this illustration were all about 20 cm. long. The figures are drawn by projection in an episcope, the fat which is stained deep red in the actual specimens being here shown as black.

through the middle of a vertebra or passed between two of them. Variation in the level of the cut, however, never affected the general appearance of fatness; it did not expose so much more or so much less fat as to make a fish appear fatter or leaner than it would if sliced in another plane. The two faces of a slice always corresponded closely although they would rarely be cut at the same vertebral level. In judging fatness both faces of a slice were taken into consideration. After some experience it became easy to allot each fish to one of nine arbitrary degrees of fatness. Five primary degrees were chosen, none (degree 1), little (3), medium (5), fat (7), and very fat (9); between these are the intermediate degrees 2, 4, 6 and 8. The five primary degrees are diagrammatically illustrated in Fig. 1 drawn from actual slices selected as typical, and optically projected by an episcope so that the outlines of the fat areas could be accurately traced. These drawings, together with actual type specimens, were used for comparison when assessing a sample of newly stained slices.

The accuracy of the method just outlined was checked from time to time by reassessing samples of fish the original records of which were not remembered. It always happened that not less than 80 % of the fishes comprising the sample were given the same degree as before; the remainder would be placed one degree higher or lower, about half of them higher and about half of them lower. Very occasionally an odd fish would be moved two degrees up or down the scale of nine. Thus the method was well within the limits of error which could be allowed.

The main results based on the large slices were supplemented by cutting frozen sections from as many fish as possible. Large pieces of tissue were removed from the pigmented upper side half-way between head and tail. The pieces were generally obtained from large slices which had been previously cut and stained. The tissue was taken in the region of the lateral septum, extending some way on either side and down to the vertebral column. From each piece of tissue generally three, sometimes more sections were stained and mounted. Some were also cut from the region of the dorsal and anal fins after removal of the bones.

For cutting, the tissue was surrounded by an aqueous solution of gelatine (5 %) and the sections allowed to fall into a dish of the same solution kept just melted by gentle heat. Selected sections were stranded on clean slides, cooled and hardened first in formalin vapour and then in 5 % formalin. The sections thus stuck to the slides were stained in Scarlet Red dissolved in equal parts of 70 % alcohol and acetone. The sections were permanently mounted in glycerine sealed by glycerine jelly and "Murrayite". They have kept very well to date.

The sections were cut 150 μ thick. Thinner sections were useless as the fat cells are relatively large and most of the fat is lost when their membranes are ruptured. By cutting thick sections fat loss was relatively reduced. The sections were thin enough for easy observation by transmitted light.

Distribution of the Adipose Tissue

In this paper attention is confined to the fat and adipose tissues in and around the edible muscular portions of the flounder, and to some extent of its skeleton. The head and viscera are neglected.

Adipose tissue is developed in definite regions. The largest and most striking are clearly visible in a stained slice across the body of the fish; they are the fatty regions of the dorsal and ventral unpaired fins. The muscles to the fin rays are packed around with fatty tissue filling up the spaces which might otherwise be left between them. In a skinned fish which has been preserved in formalin, or in one that has been boiled, this adipose tissue is distinguishable from the whiter muscles by its yellow brown colour. This colouration seems to have misled Stirling (1886) into describing the tissue as red muscle, both in the plaice and in the flounder. In really fat fish much fat is deposited in these regions, padding out the edges of the fish so that they feel plump between the fingers. On the other hand a lean fish, particularly one which has lost all its fat at spawning, feels thin and even looks emaciated where the median fins join the body. In such a fish the adipose tissue is in a soft and collapsed condition owing to the withdrawal of the fat it formerly held.

There is generally a little fat between the skin and underlying muscles. Where the lateral septum joins the skin there is often a considerable accumulation which in transverse section (Fig. 2 A) frequently appears as a roughly triangular area bisected by the septum itself. There are similar deposits of fat where the myocommata reach the skin (Fig. 2 B). Adipose tissue extends down the myocommata in the region of the superficial lateral muscle and is often well developed where the myocommata join the lateral septum. Where the myocommata pass through the deep lateral muscle adipose tissue is generally absent, but in fat fish a little fat is deposited here and there.

The skeleton is a fat depot of some importance, particularly the vertebral column. The spongy parts of the vertebrae and their hollows are frequently heavily laden with fat, and so are the grooves and canals of the neural and haemal spines. Adipose tissue is often present around the bones. The bones of the skull may also be laden with fat.

Groups of fat globules are present in the skin among the chromatophores, but the quantity of fat so stored is very small in comparison with that in the depots already described.

Fat is distributed in a closely similar manner in many flat-fishes. Several specimens of each of the following species have been examined. *Pleuronectes platessa*; *P. limanda*; *P. microcephalus*; *Rhombus laevis*; *Lepidorhombus whiff*; *Arnoglossus laterna*; *A. imperialis*; *Solea vulgaris*. It is also very similarly distributed in *Zeus faber*.

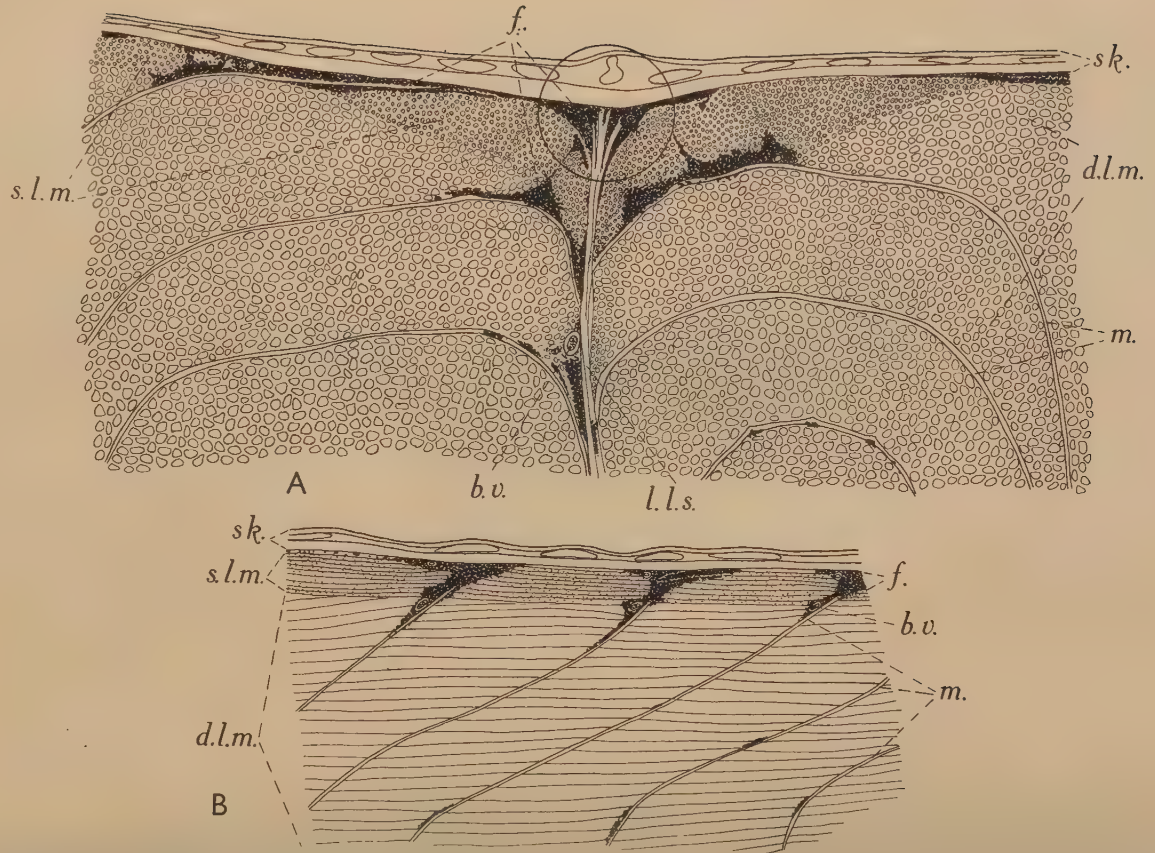


Fig. 2. Semi-diagrammatic representations of frozen sections of the muscular tissues close to the lateral line, midway between head and tail, on the pigmented side of the flounder. × 5. Fat shown in black. The circle indicates the region shown in greater detail in Fig. 5. A. Transverse section from a female caught at sea in February 1937. The fish was 35·7 cm. in length and was placed in fatness degree 8. Intramuscular fat was very plentiful in the superficial lateral muscle. B. Longitudinal section some little distance from the lateral line septum. This is from a male caught at sea in February 1938. The fish was 28·8 cm. long and was placed in fatness category 6. Intramuscular fat was very plentiful in the superficial lateral muscle. *b.v.* blood vessel; *d.l.m.* deep lateral muscle (musculus lateralis profundus); *f.* fat in adipose tissue; *l.l.s.* lateral line septum; *m.* myocommata; *sk.* skin; *s.l.m.* superficial lateral muscle (musculus lateralis superficialis).

Immature Flounders in the Estuaries

The growth and life history of the flounder in the Tamar and Lynher estuaries is discussed by Hartley (1939). The immature fish feed and grow in the estuaries for several years before they go down to the sea to spawn. These immature fish formed the bulk numerically of the catches investigated. The fatness of these immature fish was followed from February 1937 to February 1938, over five hundred fish being examined during this period. In addition some small exploratory samples were examined prior to February 1937; as far as they go they fit into the sequence here described. The results for males and females are combined since no significant difference was found between them.

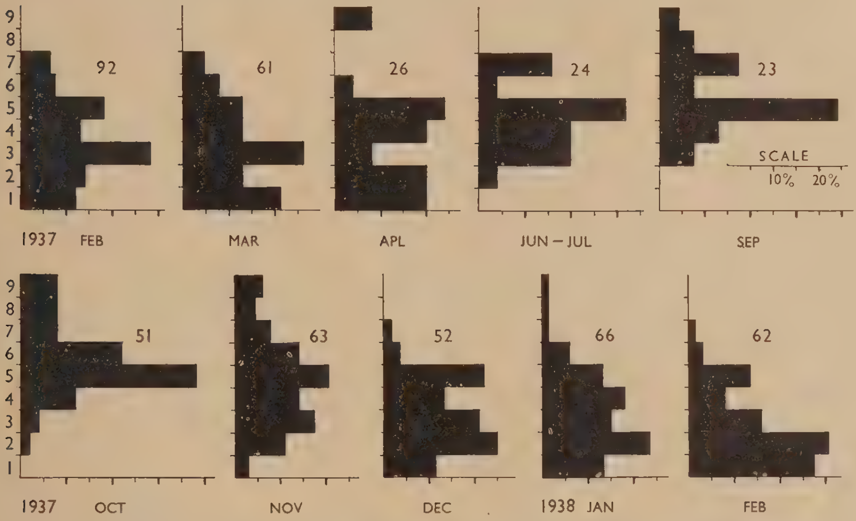


Fig. 3. The fatness of immature flounders caught in the estuaries. The ordinates are the arbitrary degrees of fatness explained on p. 364 and illustrated in Fig. 1. The abscissae are percentages. The number inserted in each figure gives the actual number of fish on which it is based.

The monthly results are given in the form of diagrams (Fig. 3). The fish were sliced and stained by the method already described. The diagrams give the percentage number in each fatness group. The number of fish on which each diagram is based is indicated in the figure.

It is at once obvious that in February 1937 the majority of the flounders had a medium (degree 5) or less than a medium amount of fat in their tissues; 12 % had none. By March the percentage with none had increased to rather more than twenty-one and the sample as a whole was a little less fat than in the preceding month, although the difference is but slight; allowing for the experimental error inherent in the method it is perhaps not significant. The first week in April showed little change; the sample was a small one in which two large immature but very fat females probably give an undue prominence to degree 9 in the diagram. As explained by Hartley (1939), it was difficult to catch flounders during the summer and the samples taken then were all small. Only one fish was caught during May; it was of medium fatness (degree 5). The immature fish of June and July are combined in the one diagram. It is notable that in no fish caught during these months was fat entirely absent, while the general fatness of the sample was higher than before. In August a very few fish were caught but it is worth recording that of the four immature ones obtained three were fat (degree 7) and one medium to fat (degree 6). In September and October immature flounders reached their maximum fatness for the year. It is apparent from the diagrams that the majority were of medium fatness (degree 5) and over, a striking contrast to the condition of February, March and April fish. In November fatness was on the decline, and once again a few fish were found with no visible fat at all. December and January fish were on the whole definitely lean, while in February 1938 the leanest sample of the series was obtained, over half the fish having either no fat at all or very little indeed.

It is possible to work out a mean degree of fatness for each monthly sample: these means are presented in the first column of Table I. Again it will be seen that the immature fish fatten from March to September and October when the maximum is reached and then steadily lose fat until the following February.

TABLE I. MEAN DEGREES OF FATNESS OF IMMATURE FLOUNDERS

		Total fish	Fish under 16 cm.	Fish over 16 cm. and under 20 cm.	Fish over 20 cm.
1937	Feb.	3·6 (92)	3·1 (33)	3·8 (42)	3·9 (17)
	Mar.	3·3 (61)	2·9 (41)	3·5 (28)	4·3 (18)
	Apr.	3·7 (26)			
	May	..	..	..	..
	June	4·2 (24)	3·9 (9)	5·0 (7)	5·1 (8)
	July				
	Aug.	..	..	..	..
	Sept.	5·6 (23)	5·0 (23)	6·0 (34)	5·6 (17)
	Oct.	5·6 (51)			
	Nov.	4·7 (63)	4·3 (6)	5·1 (36)	4·2 (21)
	Dec.	3·3 (52)	3·0 (63)	3·5 (30)	3·9 (25)
1938	Jan.	3·3 (66)			
	Feb.	2·6 (62)	2·5 (35)	2·6 (10)	3·0 (17)

The numbers in brackets give the actual number of fish on which each mean is based.

The size range of the immature fish was considerable. Most of them were over 10 cm., but less than 20 cm. in length. A few were less than 10 cm. long. Of those which exceeded 20 cm. only a very small number were longer than 25 cm., the largest of all generally being female.

In order to ascertain whether fatness varies to any extent with size, the fish have been grouped into three classes according to length. The limits of each size group are somewhat arbitrarily selected, but a limit at 16 cm. divides almost equally the yearly total of fish less than 20 cm. long, although it will be seen from Table I that in any one sample there are usually more of one length class than of the other. It is not as a rule until they are longer than 20 cm. that flounders mature and go down to the sea. The mean degree of fatness was calculated for each size group for each month, or for two months combined. These figures are given in Table I.

It will be observed that though there is little to choose between the relative fatness of the three size groups, the under 16 cm. group are consistently leaner than the 16–20 cm. fish, and in all but one month (November) leaner than the fish over 20 cm. The latter have a slightly higher mean than the 16–20 cm. fish except in the combined September and October groups and in November. Although the significance of this difference is uncertain as the numbers of fish were small, there is nevertheless the possibility that a proportion of the fish over 20 cm., which would previously have been ranked as immature, are in the period September to November sufficiently far advanced in maturity to be then recognized as maturing flounders and would therefore no longer be counted among the immatures. Such fish would be likely to be among the fattest in the sample and their removal would bring about a lowering of the mean.

On one point the means for the three length groups are quite definite; they demonstrate conclusively that the annual cycle of fatness in immature fish over 10 cm. long takes place irrespective of size.

MATURING AND SPAWNING FLOUNDERS

Maturing and spawning flounders leave the Tamar and Lynher estuaries early in the year and by the end of February only immature fish remain. It is possible to distinguish the ripening fish, or at least some of them, during the preceding summer: in the later months of the year this can be done with greater certainty as the gonads become more swollen. Ripening estuarine fish are always relatively large, the females generally exceeding 25 cm. in length, though the males are often smaller than this. The fatness records for maturing estuarine flounders are presented graphically in Fig. 4 *a–c*, and the means based on the same figure are given in Table II. As the total number

TABLE II. MEAN DEGREES OF FATNESS OF MATURING AND MATURE FLOUNDERS

	Mean degree of fatness	No. of fish
Estuarine fish:		
June, July and August 1937	7·0	11
November and December 1936 and 1937	7·0	30
January and February 1937 and 1938 ...	6·1	33
Sea fish:		
February 1937 and 1938	6·5	75
March 1937 and 1938	4·7	62
April 1937 and 1938	2·4	29
Females returned to the estuaries after spawning:		
May–August 1937	6·4	7

of fish was rather small two years are combined. There was no marked difference between corresponding months of the two years when each year was considered separately.

If the fatness of these ripening fish be compared with that of immature flounders for the corresponding seasons it will be seen that they are much fatter. The mean for the summer months is 7·0, a figure never reached by the immature fish. It is conceivable that this may be exceeded during September and October at which time immature fish are fattest. Unfortunately all large fish caught during those months were required for marking experiments and there are therefore no fat records available. The mean is, however, still 7·0 during the last two months of the year, a period when immature fish rapidly lose fat. By January and February, however, there has been a slight decrease in the fatness of those maturing fish which have not yet moved down to the sea.

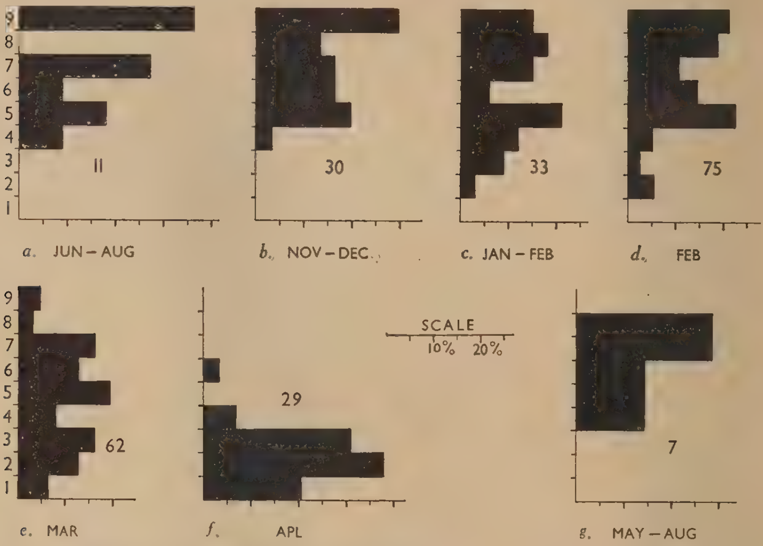


Fig. 4. The fatness of maturing and spawning flounders. *a–c*, fish caught in the estuaries; *d–f*, fish caught at sea; *g*, females caught in the estuaries after spawning. *a* is based on fish caught in 1937 only; *b* on fish caught in 1936 and 1937; *c–f* on fish caught in 1937 and 1938; *g*, on fish caught from May 29 to August 9, 1937. The scales are as in Fig. 3.

A few flounders were caught at sea during January, but it was not until February that they were at all numerous in the trawl. While some of these would have come from the estuaries a short time before capture, it is possible that some had been in the sea since at least the preceding season. Unfortunately we know nothing of the life of such fish in the sea; as Hartley (1939) points out, flounders are rarely taken in the trawl out of the breeding season.

Ripe and ripening sea-fish during February generally have plenty of fat in their tissues although a few are quite lean. The mean is high (6·5), for these fish as a whole are relatively fatter than are immature fish at their best during the late summer months, while they are, of course, very much fatter than are immature fish during February. This fat is, however, rapidly used up during the spawning period so that in April, by which time the fish are quite ripe or have already spawned, sea flounders are very lean indeed. The loss of fat is so rapid that the adipose tissue presents a collapsed appearance, sections showing crumpled cell walls enclosing no fat at all or only a few droplets. It will be noticed that in two months the figure for mean fatness falls from 6·5 to 2·4, whereas in immature fish it takes at least four months for the mean to fall through the smaller range of 5·6–2·6.

It would be instructive to find out if possible whether the loss of fat during the spawning period is at all accelerated during the presumably strenuous act of shedding eggs or sperm. The figures denoting mean fatness for February, March and April (Table II) include partly spent and spent fish. If we work out the mean fatness of these spawning and just spawned fish we get the following figures, the number in brackets indicating as usual the actual number of fish on which each mean is based: February, 5 (1); March, 4 (18); April, 2·4 (9). Ignoring February when only one spent fish was obtained it will be seen that while the figure for March is appreciably lower than the mean for all March sea fish combined, that for April is exactly the same. From this last result it seems likely that the decrease in fatness is a process not particularly accelerated by exhaustion during spawning. The lower mean for spent and partly spent fish in March may perhaps be simply due to these fish being a little in advance of the others in maturity, or as the difference is small it may not actually be significant.

Recovery of Spent Fish

Relatively few spent fish are caught in the sea, and these are nearly all obtained in March and April. After April they are not caught at all when trawling at sea, perhaps because they move too close inshore (Hartley 1939). Some of them perhaps die shortly after spawning. A few females, but apparently no males, make their way back to the estuaries and may there be caught in the tuck-nets, when they are easily recognized as spent by the condition of the gonad. Seven such females have been examined; they were caught on different dates between and including May 29 and August 9, 1937. Their mean fatness was high (see Table II and Fig. 4 *g*); the loss at spawning had evidently been made good rapidly. The histological difference between their tissues and those of ripe fish is dealt with below.

The Region of the Superficial Lateral Muscle

Frozen sections of the superficial lateral muscle region of the dark side halfway between head and tail were cut from one hundred and thirty-eight flounders selected as typical specimens of both sexes caught at all seasons of the year, both mature and immature fish. These were sufficient to give some idea of the histological distribution of the fat in this important region and of its seasonal changes.

The distribution of the subcutaneous fat and that on the myocommata as seen in these sections has already been described (p. 365). The fat is present in the form of liquid globules each enclosed within a fine membrane, the wall of the fat-storing cell. When the cell is fully loaded the wall is difficult to distinguish, but when the cell loses fat, as during spawning, it is more readily visible (Fig. 5 *c*). Large globules may be as much as 125 μ in diameter, but most of them are of various sizes smaller than this. In very fat fish the globules all tend to be large (Fig. 5 *a*) and are so closely packed as to be distorted by pressure against one another. In leaner fish the globules are on the whole smaller and not so numerous, but nevertheless they may be closely packed and distorted (Fig. 5 *b*), the difference in the amount of fat between a lean fish and a fat one being due as a rule mainly to the smaller amount of adipose tissue in the former and not so much to a wider spacing of the globules (compare *a* and *b* in Fig. 5). This is particularly true at the season of maximum fatness, but it does not hold good for fish which have recently lost much fat from their tissues. At the end of the spawning season the globules are often spaced apart and, because they are no longer pressed against one another, they round up within their cells (Fig. 5 *c*). In fish which have suffered severe fat loss globules are not only much reduced in size, some being minute, but they are often rather widely spaced apart due to the complete absorption of many others (Fig. 5 *e*). The absorption of the fat brings about a collapse of the adipose tissue cells which are crushed and crumpled between skin and muscles. Immature

---

Fig. 5. Semi-diagrammatic representations of the muscular and fatty tissues cut transversely near the junction of the lateral line septum with the skin. The area shown is indicated approximately by the circle in Fig. 2 A. The sections were stained in scarlet red and mounted in glycerine. For full explanation see text. *a*, from a ripening male. Tamar estuary November 1937. Length 21·5 cm. Fatness degree 9. A moderate amount of intramuscular fat was present but is not shown in the figure. × 22; *b*, from a ripening male. Tamar estuary November 1937. Length 21·0 cm. Fatness degree 5. A little intramuscular fat was present but is not shown in the figure. × 22; *c*, from a ripe female, caught at sea February 1938. Length 36·6 cm. Fatness degree 5, showing evidence of considerable fat absorption. Intramuscular fat was plentiful in most fibres of the superficial lateral muscle. A few clear fibres are seen. × 92; *d*, a few fibres of the superficial lateral muscle showing arrangement of the intramuscular fat droplets. From a ripening female caught at sea in February 1937. Length 35·7 cm. Fatness degree 8. × 350; *e*, from a ripe female caught at sea in March 1937. Length 34·9 cm. Fatness degree 5. Fat globules small and scattered, evidence of much absorption having taken place. A considerable amount of intramuscular fat was present but is not shown in the figure. × 14; *f*, from a female which had returned to the Tamar estuary after spawning. Caught June 1937. Length 34·7 cm. Fatness degree 7. No intramuscular fat was present. × 14.

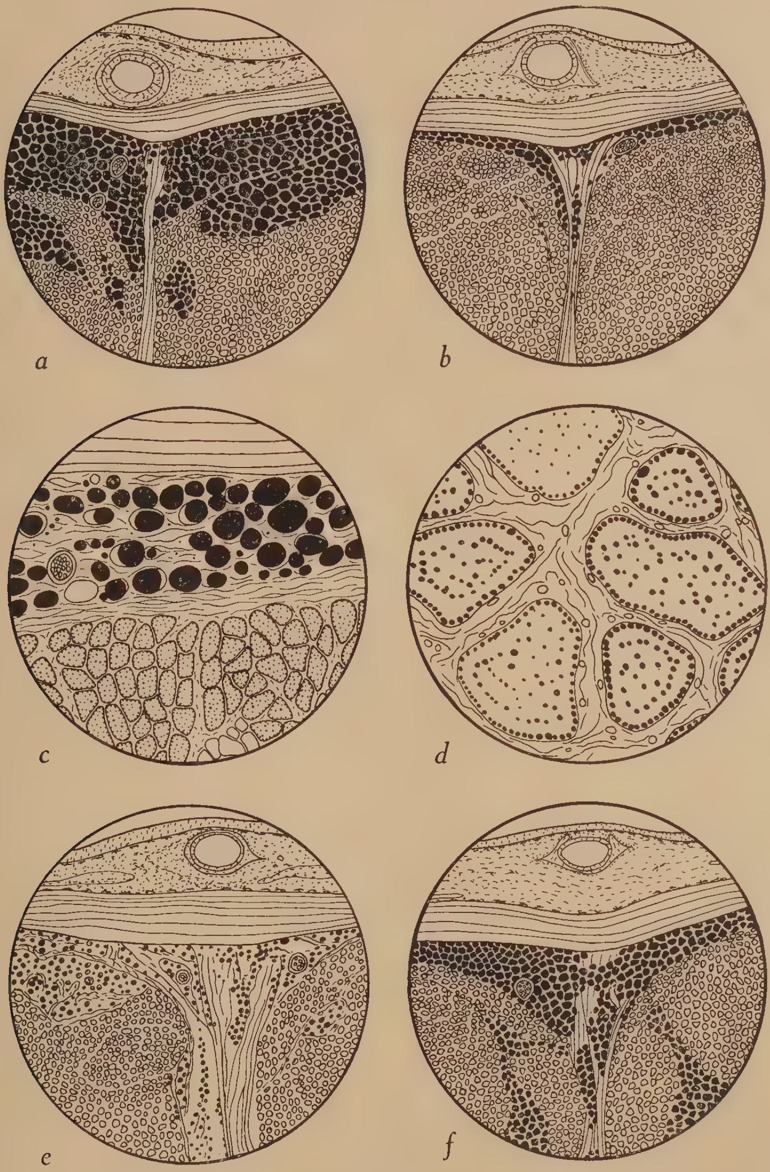


Fig. 5.

estuarine fish at the end of the winter show similar evidence of fat reduction, but to a less extent, the globules then not being on the whole quite so large and tightly packed as in September and October. In some individuals during February and March the globules are tiny, rounded and well separated. Thus the seasonal and spawning variations in general fatness can be followed, as might perhaps have been expected, in the histology of the adipose tissue of a particular body region.

Although histological investigation has been concerned chiefly with the superficial lateral muscle region, sections of the fat reservoirs between the dorsal and anal fin muscles have been cut from a few individuals. The condition of these depots appears to correspond exactly with that of the adipose tissue under the skin. In fish which have lost much fat during the spawning period the fat globules are all very small, rounded and widely scattered among empty and crumpled cells, just as they are in the mid-lateral region. It has already been remarked that loss of most of the fat in this region of a formerly fat flounder can be detected in the entire fish (p. 365). The withdrawal of much of the fat leaves the tissue readily compressible between finger and thumb. This is still more easily observed while handling large slices across the middle of the fish.

Fat is withdrawn from the skeleton about the same time as from the other depots. On account of the difficulty of sectioning this region it has not been examined in histological detail.

At certain times and in certain individuals, fat droplets appear inside most of the fibres forming the superficial lateral muscle. In the king salmon (Greene, 1914) this muscle similarly carries drops of intramuscular fat, only in much larger quantity. This is in addition to a large quantity of intermuscular fat between the fibres; the total amount of fat of both types being relatively enormous. In the flounder there is no intermuscular fat in either the superficial or deep lateral muscles, but the presence of intramuscular fat droplets at certain times is very interesting and merits attention. So far as I am aware, such intramuscular fat has been described only for the salmon. I have, however, seen fat droplets in large numbers in the fibres of the superficial lateral muscle of quite small specimens of the hake, *Merluccius merluccius* (L.). They do not seem to occur in the much fatter herring, but doubtless other fish will be found to possess them.

Intramuscular fat droplets are most strongly developed in sea flounders during the spawning period. The droplets are generally no more than 2 or 3 μ in diameter and are frequently less, but occasionally in a few fibres, perhaps in different parts of the same fibre, they reach a larger size and may be as much as 7 or 8 μ across; rarely they are larger still. A transverse section of a fibre (Fig. 5 *d*) generally shows a ring of droplets immediately under the sarcolemma with others scattered rather uniformly in the main body of the fibre itself. Both in size and distribution within the fibre they correspond closely to the description Greene has given for the king salmon.

During summer months no intramuscular fat is visible in the majority of estuarine fish, both maturing and immature. The cytoplasm of the muscle also takes up little or no stain, being clear and almost colourless in appearance in the preparations. In the autumn, however, this muscle sometimes stains pale pink with Scarlet Red and in some fish intramuscular fat droplets are to be seen. These droplets are very pale in colour, suggesting that when they first appear they contain little true fat. During the winter immature fish vary in condition; in some the cytoplasm is unstained, such fish having as a rule no intramuscular fat or at most very little. In others the cytoplasm stains pink and these fish generally have intramuscular fat droplets, occasionally in abundance. Maturing fish at this time nearly all show a pink staining of the cytoplasm and have fat droplets in the fibres, in a few individuals these are in large numbers. The concentration of intramuscular fat in the immature fish shows little or no increase beyond the winter condition, but in mature fish from the sea during February and March much of it is found, the droplets staining much more deeply at this time than before. The cytoplasm too is generally stained pink, often quite deeply. Only exceptionally in such fish is there no intramuscular fat. This condition of strongly stained cytoplasm and much intramuscular fat persists until after spawning. Even in fish which have lost most of the fat from their adipose tissue the superficial lateral muscle stains quite deeply and contains fat droplets in abundance. This fat is evidently not reduced in quantity while that from the adipose tissue is being used up. It is nevertheless soon lost; females which have returned to the estuaries after spawning show clear unstained cytoplasm (like most other summer fish) and no intramuscular fat—or at most only a trace. These latter fish are generally fairly fat, their adipose tissues being well laden with large globules closely crowded together (Fig. 5 *f*). The absence of fat from their superficial lateral muscle fibres is therefore not due to lack of fatty materials at that time. The immature fish in the estuaries also lose their intramuscular fat about the same time.

The foregoing description of the intramuscular fat cycle is only a brief sketch of changes followed with the aid of a single stain; an insufficient number of fish have been sectioned for a complete account to be given. Microchemical investigation is desirable before attempting seriously to discuss its implications. It may be noticed, however, that while this intramuscular fat is most strongly developed in mature sea fish, and might possibly be related to the maturation of the gonads, it also appears in immature fish, although to a less extent, about the same time. Hartley (1939) has shown that there is sometimes to be observed a spurious ripening among immature flounders. The presence of intramuscular fat can also, of course, be correlated with temperature, and perhaps with other conditions of the environment as well.

DISCUSSION

We have seen that immature flounders are fattest at the end of the summer and leanest at the end of the winter. This refers to the population as a whole, for at any one time some fish are much fatter than others of the same size and sex. Sex appears to have little effect on general fatness, while there is only a slight tendency to greater fatness with increase in size. No doubt some individual flounders are naturally lean while others have an equally natural tendency to store fat in their tissues; this is probably to some extent independent of the amount of food consumed. It seems legitimate to assume, however, that after a period of intensified feeding lean fish will be fatter than usual and naturally fat fish very fat. During periods of starvation both types of fish may be expected to use up some or all of their fat reserves. With this idea in mind we can correlate seasonal variation in fatness with feeding.

Hartley has examined the stomach contents of the flounders used in these fatness determinations and he has shown (1939) that the immature fish have a marked period of fasting during the winter and that this fast is not completely ended until probably April. This period when little food is taken is that during which immature flounders lose much of their autumn fat. In the winter of 1937–8 Hartley found that the fast began earlier than in the preceding year, and to this may perhaps be correlated the greater leanness in February 1938 as compared with February 1937. During the summer and until September feeding is most intense; it is at the end of this period that the immature fish are fattest.

Maturing and mature flounders behave differently for they continue to feed throughout the fasting period of the immature fish, only ceasing to take food during the spawning season in the sea. To these habits again fat content may be correlated, maturing flounders remain very fat until the end of the year and then show a rapid loss while breeding. During spawning a great deal of energy is probably expended in muscular and other activities; abstention from food at this time will cause a heavy demand upon the fat reserves, and, as we have seen, they are depleted very rapidly.

It might be expected that in maturing fish fat would be withdrawn from the tissues during maturation of the gonads, which in the female especially accumulate a great quantity of fatty substances. The fat for the gonads, however, may come from the visceral fat which has not been investigated during the present work. It should be remembered too that the fish are continually feeding while the gonads are filling. At any rate the gonads reach their full size before there is any loss of fat from the muscular regions. This is in agreement with what is known of the herring where it appears not improbable "that the metabolic demands of the growing gonads are met, in the first instance by the fatty reserves of the liver, while at a later stage the stores of mesenterial fat may be called upon. There is no evidence that the fat of the muscular tissue undergoes depletion, until shortly before the time of spawning" (Bruce, 1924, p. 483). Johnstone (1918) found that in the herring maturation of the gonads is accompanied by an increased loading of the subdermal and intermuscular connective tissues with fat, and that this loading does not decrease until a short time before spawning and "after the major part of increase in mass of the gonads has taken place". As is well known, herring do not feed while spawning. More recently Channon and El Saby (1932) have shown that in maturing herring the muscle fatty acids continue to increase in amount after those of the liver and mesentery have begun to decrease.

Johnstone (1915, 1918) emphasized the importance of temperature as a factor in influencing variations undergone by the tissue fat. He showed the close correspondence between sea-temperature and rise and fall of fat content, and argued that temperature must be a factor in addition to the sexual cycle. Thus Clyde winter-spawning herring maturing in cooling water have a considerably lower maximum fat content than the Manx autumn spawners. He had little to say about feeding. The close correlation between fatness and feeding is discussed in a recent paper by Lovern & Wood (1937). The facts are strongly reminiscent of those already pointed out for the flounder.

The effect of seasonal temperature variations on the flounder is probably reflected in the intensity of the feeding of immature fish. It is while the temperature is rising and during the period when it is presumably maximal that feeding is most intense, with a corresponding effect on the fat reserves. The winter fast begins while the temperature is falling. Maturing fish, on the other hand, continue to feed while the temperature is falling and any effect on them is not apparent.

With the immature flounder can be compared the immature plaice. Johnstone (1918) records that in plaice less than 30 cm. long the weight per unit of length varies regularly with the sea-temperature, the plaice being heaviest for their length when the sea-temperature is maximal and lightest when it is minimal. Hartley (1939) has worked out a similar condition factor for the flounder and the same relation is apparent although he does not specially distinguish between immature and mature fish. Hartley's condition factors correspond fairly closely with the figures for mean fatness if due allowance be made for the fact that they are not tabulated on quite the same basis.

Bruce (1924) found that the fat content of herring muscle at any given stage of maturity is increased by age. Lovern (1938) has recently stated that the fat content of the freshwater eel "increases almost linearly with length, at any rate between certain limits". Bruce's and Lovern's findings are based on chemical analyses. It has been seen that in the immature flounder a size increase also brings about a slight general fattening as measured histologically. An insufficient number of mature fish are available for a good comparison to be made between their smaller and larger sizes. The figures that are available suggest that there is very little tendency to increased fatness with size.

Some further comparisons of the intramuscular fat of the flounder with that of the king salmon are of interest. It will be remembered that in the flounder fat in the fibres of the superficial lateral muscle is apparently not drawn upon while that of the normal adipose tissue is removed during the last stages of maturity (p. 375); it disappears last of all. In the salmon (Greene, 1914) there is a very large load of intramuscular fat at the beginning of the long migration; this is gradually used up during the journey but is not completely removed and even at death a considerable quantity is still present. The deposition of fat in the superficial lateral muscle of the salmon begins in embryonic life and increases in amount up to the time of cessation of feeding. The deep lateral muscle on the other hand does not show fat droplets inside its fibres until the salmon ceases to feed early in the journey to the spawning grounds. These droplets thus appear at a maturity stage corresponding very roughly with that in the flounder at which the intramuscular fat develops in the superficial but not the deep lateral muscle. The droplets in the deep lateral muscle of the salmon maintain a relatively uniform distribution in the fibres until death. Greene infers that the fat in the fibres is utilized in the production of muscular energy expended during the migratory journey up river. He suggests that this intramuscular fat is maintained at its uniform distribution by a continual replenishment from the intermuscular fat depots and those of the adipose connective tissues which are depleted during the migration. He argues that with the cessation of feeding the products of digestion no longer reach the active musculature, and that there is then thrown into the deep muscle fibres a supply of fat adequate to the energy needs. Reference should be made to Greene's own paper for details of his hypothesis to which he devotes much space.

Comparing salmon and flounder it is evident that the superficial lateral muscle has a much greater potentiality to the deposition of fat droplets in its fibres than has the deep lateral muscle. In the salmon it early begins the accumulation of what eventually becomes a great store of fat; the deep muscle on the other hand does not have an intramuscular loading until very much later and it is never as great as that of the superficial muscle at its maximum. In the flounder the superficial lateral muscle is the only one of the two lateral muscles ever to acquire droplets of fat in its fibres. They are most strongly developed in mature fish, especially after cessation of feeding. They also occur in some immature fish and it may be significant that it is during or just after the winter fast that they are most numerous. In all classes of flounder during the summer when they are intensively feeding these droplets are almost entirely or quite absent. It may be that in all fishes the superficial lateral muscle has a greater tendency to store fat than has the deep lateral muscle. The fat may not always be detectable by histological techniques; it may be in a form recognizable only by chemical extraction. The fact that no droplets are to be seen in the fibres of any particular fish does not necessarily mean that there is no fat there at all. A seasonable comparison between superficial and deep lateral muscles of many types of fishes carried out biochemically and checked histologically might yield interesting results.

SUMMARY

In the flounder adipose tissue forms a padding between the muscles to the dorsal and ventral fins. A little is present under the skin, more especially where the lateral line septa and the myocommata meet the skin. In addition a quantity of fat is associated with the skeleton.

Immature flounders living in the estuaries of the Tamar and Lynher are fattest after intense feeding during the summer, and leanest after the winter fast.

Maturing flounders have a high fat content before going to sea to spawn. While in the sea during the spawning season, February to April, very little feeding takes place and there is a rapid drop in fat content. Spent fish are very lean.

Those females which return to the estuaries after spawning rapidly make good their fat loss.

There is considerable individual variation in fatness irrespective of seasonal and spawning variations.

Large fish tend to be slightly fatter relatively than small. General fatness does not appear to be affected by sex.

In some individuals the fibres of the superficial lateral muscle contain numerous fat droplets during the autumn and winter. They are not present as a rule during the summer. These intracellular droplets are a striking histological feature of mature sea fish during the spawning season.

REFERENCES

BJERKAN, P., 1917. Age, maturity and quality of North Sea herrings during the years 1910–13. *Rep. Norweg. Fish. Mar. Invest.*, Vol. III, No. 1, pp. 1–119.

BRUCE, J. R., 1924. Changes in the chemical composition of the tissues of the herring in relation to age and maturity. *Biochem. Journ.*, Vol. XVIII, pp. 469–85.

CHANNON, H. J. & EL SABY, M. K., 1932. Fat metabolism of the herring. I. A preliminary survey. *Biochem. Journ.*, Vol. XXVI, pp. 2021–34.

GREENE, C. W., 1914. The storage of fat in the muscular tissue of the king salmon and its resorption during the fast of the spawning migration. *Bull. Bureau Fisheries Washington*, Vol. XXXIII, pp. 69–138.

GREENE, C. W. & GREENE, C. H., 1914. The skeletal musculature of the king salmon. *Bull. Bureau Fisheries Washington*, Vol. XXXIII, pp. 21–59.

HARTLEY, P. H. T., 1939. The Saltash tuck net fishery. A contribution to the ecology of estuarine fishes. (In Press.)

HJORT, J., 1914. Fluctuations in the great fisheries of northern Europe. *Rapp. Proc.-verb. Int. Cons. Explor. Mer*, Vol. XX, pp. 1–228.

JOHNSTONE, J., 1915. The fat content of Irish Sea herring. *Proc. and Trans. Liverpool Biol. Soc.*, Vol. XXIX, pp. 216–23.

—— 1918. The dietetic value of the herring. *Proc. and Trans. Liverpool Biol. Soc.*, Vol. XXXII, pp. 85–131.

LOVERN, J. A., 1938. Fat metabolism in fishes. XIII. Factors influencing the composition of the depot fat of fishes. *Biochem. Journ.*, Vol. XXXII, pp. 1214–24.

LOVERN, J. A. & WOOD, H., 1937. Variations in the chemical composition of herring. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 281–93.

STIRLING, W., 1886. On red and pale muscles in fishes. *4th Ann. Rep. Fish. Board Scot. for the Year* 1885, pp. 166–71.

ON THE SEASONAL ABUNDANCE OF YOUNG FISH. VI. THE YEAR 1938

By F. S. Russell, F.R.S.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–3)

The present report continues the series of observations on the seasonal abundance of the pelagic young of teleostean fish in the plankton off Plymouth (Russell, 1938*b*), and gives the results for the year 1938. These results are published in the same form as in previous reports. The dates on which collections were made with the 2 m. stramin ringtrawl are given in Table I, and the monthly average catches of the young fish per half-hour oblique haul in Table II. In Fig. 1 is given the curve for the average catches for each fortnight of all young fish, excluding clupeids, and superimposed upon this the corresponding curve for the average catches over the period 1930–4 inclusive.

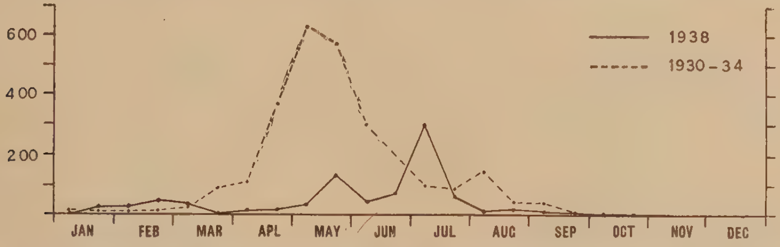


Fig. 1. Curves showing the average catches in half-hour oblique hauls with the 2 m. ringtrawl for each fortnight for all young fish, excluding clupeids, in 1938 (——) and the same averaged over the period 1930–4 inclusive (-----).

The results are practically a repetition of those for 1936 and 1937. The complete absence of the peak for the young of spring spawners was repeated in 1938, and if anything their numbers were even lower than in the two previous years. The sum of the monthly average catches of those post-larvae which show maximal abundance in the months June to October inclusive, excluding clupeids, was 135 in 1938, as against 174 in 1937 and 115 in 1936. The 1938 figures should perhaps have been slightly lower as they were heavily weighted by one exceptionally heavy catch on July 5. The numbers in this catch were rather remarkable, there being 2525 clupeids and 502 other fish, while the remaining July catches gave figures of 180, 94, and 80 for all fish including clupeids. There were no *Sagitta elegans* in the catch on July 5, nor were there any indications from the plankton that the water might have been of different origin on that day as compared with other weeks in June and July. But the whole plankton catch was itself unusually large on July 5 and we can only conclude that the plankton had been collected together by some unusual condition of tidal or other currents. Lest this anomaly should cast doubt on the general picture based on these single weekly hauls it should be pointed out that during each week ringtrawl collections are made for other purposes. These collections have always confirmed the results of the routine observations.

The general poverty of young fish in 1938 again shows correlation with the low phosphorus content of the water in the previous winter, which was −16% below the mean (Cooper, 1938, p. 187).

The sums of the average monthly catches of the more important species for the year 1938 divided by the corresponding average sums for the period 1930–4 inclusive are given below. In the second column are the figures for the best year divided by the worst year from 1930 to 1938 inclusive.

	$\frac{1938}{\text{Av. 1930--4}}$	$\frac{\text{Best}}{\text{Worst}}$
G. merlangus	0·08	23·6 ('32/'36)
G. minutus	0·13	40·3 ('32/'36)
Onos spp.	1·21	13·0 ('30/'35)
Arnoglossus sp.	0·51	11·5 ('31/'34)
S. norvegicus	0·05	28·7 ('32/'38)
P. limanda	0·24	14·0 ('31/'35)
P. microcephalus	<0·04	>41·0 ('32/'38)
S. variegata	0·20	7·6 ('32/'38)
Callionymus sp.	0·14	7·7 ('30/'38)
S. scombrus	1·54	11·2 ('30/'35)
Gobiid sp.	0·05	119·0 ('30/'37)

The year 1938 has thus been the worst during the period 1930–8 for *S. norvegicus*, *S. variegata*, and *Callionymus*.

The decrease in the numbers of *Callionymus*, which was commented on in the report for the year 1937, has been continued, these having fallen from an average of 548 for the period 1930–4 to only 76 in 1938. The first column in the above table shows very clearly the decrease in the numbers of those species which were of considerable importance in the young fish population in the years 1930 to 1934. Except for *Onos*, *Arnoglossus*, and *Scomber*, all species are now less than one-quarter as numerous as they were in the period 1930–4, and, of these, half have been reduced to less than one-tenth.

If the number of young of summer spawners (135) be subtracted from the total young fish (450), we are left with 315 for the remaining young fish most of which are the young of spring spawners. This is the lowest number yet recorded and is less than one-quarter of the 1395 specimens recorded in 1931.

There are indications that this decline in production is now being shown in the stocks of adult fish.

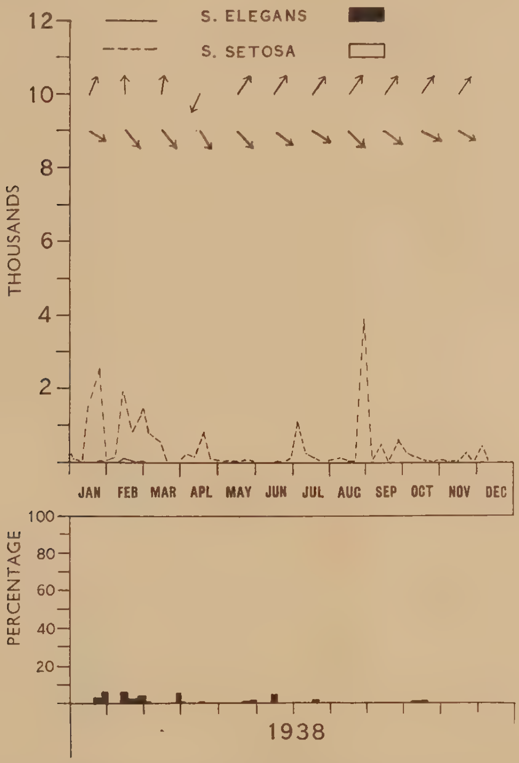


Fig. 2. Above, curves showing the actual abundance of *Sagitta elegans* (——) and *S. setosa* (-----) in half-hour oblique hauls with the 2 m. ringtrawl during the year 1938. Below, the percentage composition of the *Sagitta* populations during the same period: *S. elegans*, black; *S. setosa*, white. At the top of the diagram the arrows indicate the mean directions (true) of the flow of water past the Varne Lightship (above) and the Royal Sovereign Lightship (below) from data kindly supplied by Dr J. N. Carruthers.

As regards the plankton the conditions during 1938 were exceptional (Figs. 2, 3). There has been an almost complete absence of *Sagitta elegans*, and *S. setosa* has predominated since August 1937. This is the longest consecutive period that there has been of this nature since detailed observations were started in 1930. At the same time the numbers of *S. setosa* have been unusually low, and there has been a marked scarcity of plankton animals of all kinds in the ringtrawl catches. The total number of medusae of all species,

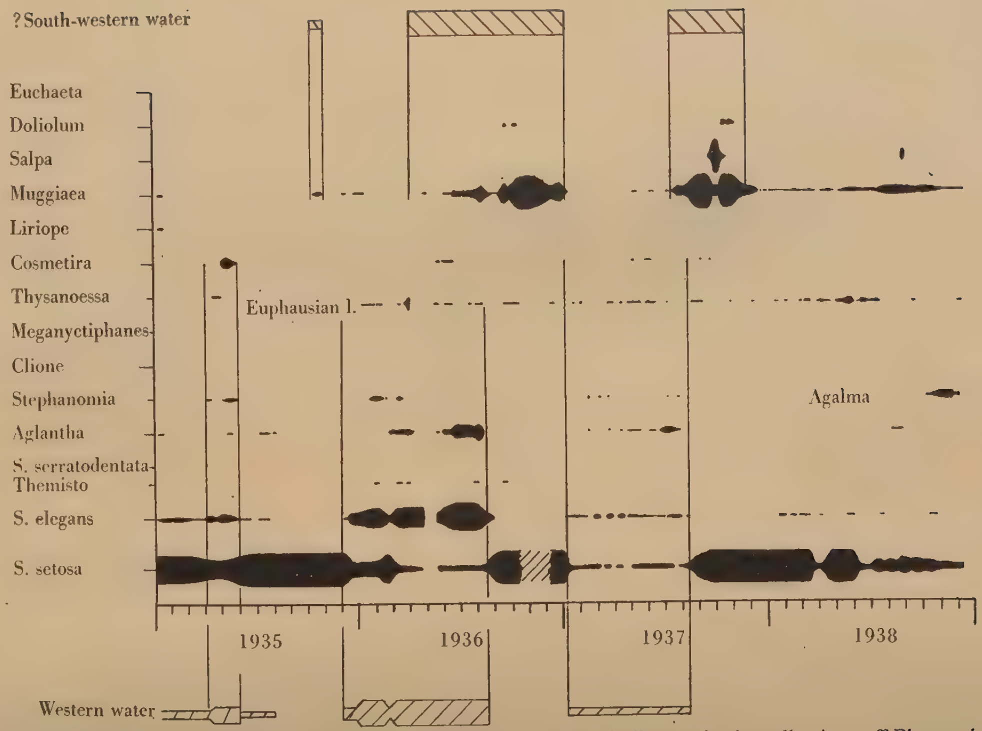


Fig. 3. Diagram showing the occurrence of the various plankton indicators in the collections off Plymouth during the years 1935 to 1938 inclusive. (Continued from Russell, 1938*b*, p. 497, Fig. 4.) The *Muggiaea* species were *M. kochi* up to January 1937, and thereafter *M. atlantica*, the salps were *S. fusiformis*, and the doliolids *D. nationalis*.

for instance, was only 2111. This is the lowest for any year since records started in 1930 (Russell, 1938*a*). It is interesting to record that the siphonophore *Agalma elegans* appeared in the catches in October and remained until the beginning of December. This is the first time that this species has been recorded from Plymouth. The species has not been accompanied by *Sagitta elegans* and it seems probable that it has been brought into the area by wind-driven surface water. It is also noteworthy that *Muggiaea atlantica* has occurred in the catches in every month of the year, although in rather low numbers.

The occurrence of many pilchard eggs was again a prominent feature. They were present from April to December, their approximate numbers, in the catches in which they occurred, being as follows. April 4 (60), 11 (160), 19 (1240), 24 (1220); May 2 (8910), 9 (3300), 17 (1700), 23 (920), 30 (1580); June 7 (2280), 14 (5540), 21 (14,120), 28 (18,180); July 5 (28,340), 11 (1380), 18 (3580), 21 (2860); August 8 (1400), 22 (30); September 6 (20), 12 (630), 19 (680), 27 (1760); October 3 (960), 10 (870), 17 (60), 25 (480); November 1 (310), 7 (1920), 14 (10), 28 (1); December 5 (1).

The pilchard eggs occurred almost to the exclusion of the eggs of other fish during this period.

REFERENCES

COOPER, L. H. N., 1938. Phosphate in the English Channel, 1933–8, with a comparison with earlier years, 1916 and 1923–32. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 181–95.

RUSSELL, F. S., 1938*a*. The Plymouth offshore medusa fauna. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 411–40.

—— 1938*b*. On the seasonal abundance of young fish. V. The year 1937. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 493–500.

TABLE I. DATES ON WHICH COLLECTIONS WERE MADE, 1938

All 2 miles east of Eddystone unless otherwise stated

Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
5	7	4*	4	2	7	5	8	6	3	1	5
10†	14	14	11	9*	14	11	15	12	10	7	9‡
17	21	18	19	17§	21	18	22	19	17	14	..
25	28	23	24	23	28*	21‖	29	27	25	21	..
31*	..	28	..	30	..	..	..	..	..	28	..

* L 4–L 5.
† Off Rame Head.
‡ L 3–L 4.
§ 4 miles W.S.W. of Rame Head.
‖ West of Rame Head.

Table II. Monthly Average Catches of Post-larvae per Half-hour

Oblique hauls with 2-m. ringtrawl, 1938

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Total young fish	24	107	22	23	149	169	845	27	12	10	11	1	1400
Ditto, less Clupeids	14	38	18	16	94	62	182	16	8	2	+	..	450
All Clupeid spp.	9	69	4	7	55	107	663	11	4	8	10	1	948
Clupea harengus	1	..	..	..	..	..	..	..	..	..	..	..	1
Gadus pollachius	..	1	..	+	3	+	..	..	..	..	..	..	4
Gadus merlangus	..	3	+	2	4	7	+	..	..	..	..	..	16
Gadus minutus	..	7	..	5	+	..	..	..	..	..	..	..	12
Gadus luscus	3	7	..	..	..	+	+	+	..	+	..	..	10
Gadus callarius	..	..	..	..	..	..	..	..	..	..	..	..	..
Onos spp.	..	..	..	+	56	4	3	+	..	..	..	..	63
Molva molva	..	..	..	..	..	..	..	..	..	..	..	..	..
Merluccius merluccius	..	..	..	..	..	..	..	+	..	..	..	..	+
Raniceps raninus	..	..	..	..	..	..	..	..	..	..	..	..	..
Capros aper	..	..	..	..	..	..	..	..	..	..	..	..	..
Zeus faber	..	..	..	..	..	..	..	..	..	..	..	..	..
Arnoglossus sp.	..	..	..	..	..	+	14	2	1	+	..	..	17
Rhombus laevis	..	..	..	..	+	..	..	..	..	..	..	..	+
Rhombus maximus	..	..	..	..	..	..	..	..	..	..	..	..	..
Scophthalmus norvegicus	..	..	..	+	1	1	1	+	..	..	..	..	3
Zeugopterus punctatus	..	..	..	..	..	..	+	..	..	..	..	..	+
Zeugopterus unimaculatus	..	..	..	..	..	..	..	..	..	..	..	..	..
Pleuronectes limanda	..	..	..	2	10	1	+	..	..	..	..	..	13
Pleuronectes flesus	..	..	..	..	..	..	..	..	..	..	..	..	..
Pleuronectes microcephalus	..	..	..	..	+	..	+	..	..	..	..	..	+
Solea vulgaris	..	1	+	1	+	..	..	..	..	..	..	..	2
Solea variegata	..	..	..	1	1	3	12	..	..	..	..	..	17
Solea lascaris	..	..	..	..	..	..	+	..	+	..	..	..	+
Solea lutea	..	..	..	..	..	1	..	..	..	..	..	..	1
Serranus cabrilla	..	..	..	..	..	..	..	..	..	..	..	..	..
Caranx trachurus	..	..	..	..	..	..	..	4	4	+	..	..	8
Mullus surmulletus	..	..	..	..	..	..	..	..	..	..	..	..	..
Morone labrax	..	..	..	..	..	..	..	..	..	..	..	..	..
Ammodytes sp.	12	19	16	1	1	1	5	+	1	1	..	..	57
Ammodytes lanceolatus	..	..	..	2	3	5	27	2	..	..	..	..	39
Cepola rubescens	..	..	..	..	..	..	..	..	..	..	..	..	..
Callionymus sp.	..	..	..	3	13	18	38	3	1	+	..	..	76
Labrus bergylta	..	..	..	..	..	2	2	..	..	..	..	..	4
Labrus mixtus	..	..	..	..	..	..	1	..	..	..	..	..	1
Ctenolabrus rupestris	..	..	..	..	..	4	13	+	..	..	..	..	17
Crenilabrus melops	..	..	..	..	..	1	3	..	..	..	..	..	4
Centrolabrus exoletus	..	..	..	..	..	..	+	..	..	..	..	..	+
Trachinus vipera	..	..	..	..	..	..	1	+	+	..	..	..	1
Scomber scombrus	..	..	..	..	..	7	26	1	..	..	..	..	34
Gobius spp.	..	..	..	..	+	..	2	..	..	..	..	..	2
Lebetus scorpioides	..	..	..	..	..	+	+	..	..	+	..	..	+
Blennius ocellaris	..	..	..	..	..	..	..	..	..	..	..	..	..
Blennius pholis	..	..	..	..	..	2	1	..	..	..	..	..	3
Blennius gattorugine	..	..	..	..	..	7	31	2	1	..	..	..	41
Chirolophis galerita	..	1	+	..	..	..	..	..	..	..	..	..	1
Agonus cataphractus	..	..	..	..	..	..	..	..	..	..	..	..	..
Trigla spp.	..	..	..	..	1	..	1	..	..	..	..	..	2
Cottus spp.	..	1	1	1	..	..	..	..	..	..	..	..	3
Liparis montagui	..	..	..	..	..	..	..	..	..	..	..	..	..
Lepadogaster bimaculatus	..	..	..	..	..	..	..	..	..	..	..	..	..
Lophius piscatorius	..	..	..	..	..	..	..	..	..	..	..	..	..
Pipe fish	..	..	..	..	..	..	..	..	..	..	+	..	+

PHOSPHORUS, NITROGEN, IRON AND MANGANESE IN MARINE ZOOPLANKTON

By L. H. N. Cooper, D.Sc., F.I.C.

Assistant Chemist at the Plymouth Laboratory

In 1936 an investigation of the inorganic constituents of certain marine zooplankton organisms was started but had temporarily to be suspended. The results obtained are presented as an interim report.

Preparation of Material and Methods of Analysis

Nauplii of the cirripede crustacean *Balanus balanoides* (sample 2) were extracted from the mantle cavities of adults on February 20 1936, by Dr H. B. Moore. Only specimens able to swim towards the light were used for analysis. These were concentrated by centrifuging, placed on a no. 50 Whatman filter, washed with 1 ml. of sea water and dried under suction before transferring to a small tared porcelain crucible. Prepared in this way the sample must contain a little sea water which will slightly affect both wet and dry (105° C.) weights. The elementary analyses reported in Table I were all made on the same dried material and are comparable. Since parallel counts of the nauplii showed wide variations, the numbers of animals attributed to the sample and the wet and dry weights of single organisms are approximate only.

Samples 9–13, from a 2 m. ring-trawl catch taken two miles off Revelstoke Point on June 5 1936, were all picked out alive with stainless steel forceps, measured, and transferred to tared glass evaporating dishes by Mr F. S. Russell. The post-larvae of the fish *Callionymus lyra* and the mature chaetognath, *Sagitta elegans*, had the following measurements:

	C. lyra	*S. elegans*
No. of animals ...	32	125
Length (mm.):		
Range	5–9	9–18
Median	7	14

Fifty ctenophores, *Pleurobrachia* (sample 11), all lay between 7 and 10 mm. in height. A further 225 animals (sample 16*a*) were taken from another catch on September 28 1936, for manganese analysis.

After removal of excess sea water by filter paper, the samples were weighed wet and then dried to constant weight at 105–110° C. Aliquot parts of dried material were weighed out on a Kuhlmann micro-balance for carbon analysis by Pregl's method, for micro-Kjeldahl nitrogen determinations by the method of Parnas and Wagner and for wet digestion for analyses of phosphorus and

TABLE I

Sample no.	Organism	Date of capture 1936	No. of animals analysed	Wet weight of one animal mg.	Dry weight of one animal mg.	$\frac{\text{Dry weight}}{\text{Wet weight}}$ %	Percentage composition based on dry weight			
							P	N	Fe	Mn
2	*Balanus balanoides* nauplii*	20. ii	102,000	0·0161	0·000915	5·67	1·7	9·7	0·12	< 0·00003
9	*Callionymus lyra* post-larvae	5. vi	32	8·72	1·23	14·1	1·60	8·24	0·031	..
10	*Sagitta elegans* mature	5. vi	125	5·71	0·530	9·29	0·945	9·24	0·042	..
11	*Pleurobrachia pileus*†	5. vi	50	115	5·09	4·43	0·230	1·34	0·0050	..
11	,, ,, (ash free)	5. vi	50	..	..	..	0·630	3·68	0·0137	..
16*a*	,, ,,	2. x	225	481	19·6	4·07	..	..	..	< 0·00005
12	Portunid megalopas	5. vi	15	4·47	0·784	17·5	1·14	6·32	0·077	..
13	Portunid zoeas and Crangonid larvae	5. vi	34	3·27	0·519	17·5	1·16	7·22	0·035	..
14	Portunid zoeas and Crangonid larvae	5. vi	20	1·77	0·301	17·0	..	..	0·093	..

* C 43·1 %, H 9·2 %, ash 16·3 %, chitin < 2 % on dry weight.

† Ash at dull red heat 63·57 %.

Sample no.	Organism	Content of one animal µg.				Ratios in mg.-atoms	
		P	N	Fe	Mn	N/P	Fe/P
2	*Balanus balanoides* nauplii	0·016	0·89	0·0011	< 0·00003	12·6	0·039
9	*Callionymus lyra* post-larvae	19·6	101	0·38	..	11·4	0·012
10	*Sagitta elegans* mature	5·02	49·0	0·22	..	21·6	0·025
11 and 16*a*	*Pleurobrachia pileus*	11·7	68·0	0·25	< 0·009	12·8	0·012
12	Portunid megalopas	8·93	49·5	0·60	..	12·2	0·038
13	Portunid zoeas and Crangonid larvae	6·05	37·4	0·18	..	13·7	0·017
14	Portunid zoeas and Crangonid larvae	..	..	0·28	..	..	..

iron (Cooper, 1935*a*, *b*). In all the samples copper was determined by the diethyldithiocarbamate method. The amounts found were always greater than records for similar animals in the literature. The detailed results are withheld until the method can be re-examined.

Manganese determinations, requiring a large amount of material, were made only on *Pleurobrachia* and on *Balanus* nauplii. *Pleurobrachia* (225 animals; 108 g. wet weight) were digested with 5 ml. conc. sulphuric acid and perhydrol drop by drop. Some green matter remaining was destroyed with potassium persulphate. The solution was diluted and filtered through sintered glass and the manganese determined by the method of Willard and Greathouse (Yoe, 1928, p. 273) in which potassium periodate is employed to oxidize manganese to permanganate.

Discussion of Results

The presence of iron and copper in all the samples (Table I) confirms Fox & Ramage's report (1931) of their ubiquity in marine invertebrates and suggests further that the occurrence of both in sea water ought to show considerable seasonal fluctuations. The analyses of iron in the plankton indicator, *Sagitta elegans*, differ strikingly from those made two years earlier on *S. setosa* (Cooper, 1935*b*).

	Date of capture	No. in sample	Average length mm.	Content of one animal (μg.) P	Content of one animal (μg.) Fe	Ratio Fe/P mg.-atoms
*Sagitta setosa**	24. v. 34	6	15	5·3	6·8	0·72
Sagitta elegans	5. vi. 36	125	13·9	5·02	0·22	0·025

* No record has been kept of the condition of the forceps used for picking out *S. setosa* from the 1934 catch. These might have been rusty.

The contents of phosphorus, nitrogen and iron in *Pleurobrachia*, even after recalculation to an ash-free basis, are all considerably lower than those of other animals examined, suggesting that its gelatinous structure must consist of carbohydrate or fatty material and not of protein. *Pleurobrachia* contained less than 2×10^{-6} % of their wet weight as manganese ($< 5 \times 10^{-5}$ %

Table II. Seasonal Changes in Iron and Phosphorus Content of Plankton

Catches taken with the quantitative net in the English Channel at Station L 4 between the surface and 45 m.

Date 1935	Content in plankton from a cubic metre of sea water: mg. Fe	mg. P	Ratio Fe/P: wt./wt.	mg.-atoms
April 3	0·73	0·602	1·20	0·68
April 23	0·96	1·16	0·82	0·46
May 8	0·85	0·64	1·33	0·74

of dry weight). Since sea water contains from 0·1 to 1 × 10^{-6} % Mn (Thompson & Wilson, 1935), this animal evidently effects no considerable concentration of manganese from sea water. *Balanus* nauplii yielded a similar result.

Table II records some analyses of iron and phosphorus in mixed plankton in the spring of 1935 which confirm the picture already found in 1934 (Cooper, 1935*b*, table IV).

I wish to express my indebtedness to Mr F. S. Russell, who provided all but one of the zooplankton samples and measured them for me, and to Dr H. B. Moore, who prepared a very clean sample consisting only of lively *Balanus* nauplii.

SUMMARY

Analyses of phosphorus, nitrogen, iron and manganese are recorded for *Balanus* nauplii (a cirripede crustacean), post-larval *Callionymus* (a teleostean fish), mature *Sagitta elegans* (a chaetognath), *Pleurobrachia* (a ctenophore) and for crab zoeas and megalopas (Table I). A sample of *Sagitta setosa* in 1934 contained much more iron than that in *S. elegans* here reported. The ctenophore, *Pleurobrachia*, is relatively poor in phosphorus, nitrogen and iron and its ash-free protoplasm must evidently be rich in either fats or carbohydrates. Neither *Pleurobrachia* nor *Balanus* nauplii effect any appreciable concentration of manganese from sea water.

REFERENCES

COOPER, L. H. N., 1935*a*. The determination of phosphorus and nitrogen in plankton. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 755–60.

—— 1935*b*. Iron in the sea and in marine plankton. *Proc. Roy. Soc.*, B, Vol. 118, pp. 419–38.

FOX, H. M. & RAMAGE, H., 1931. A spectrographic analysis of animal tissues. *Proc. Roy. Soc.*, B, Vol. 108, pp. 157–73.

THOMPSON, T. G. & WILSON, T. L., 1935. The occurrence and determination of manganese in sea water. *Journ. Amer. Chem. Soc.*, Vol. 57, pp. 233–6.

YOE, J. H., 1928. *Photometric chemical analysis.* Vol. I. Colorimetry. New York: John Wiley.

THE ECOLOGY OF THE TAMAR ESTUARY

V. UNDER-WATER ILLUMINATION. REVISION OF DATA FOR RED LIGHT

By L. H. N. Cooper, D.Sc. and A. Milne, M.A., Ph.D.

From the Plymouth Laboratory

When the Pulfrich photometer is used to measure absorption of light by a turbid estuarine or sea water, the true extinction coefficient for light of a given wave-length

$$\mu_{SW} = \mu_M + \mu_{DW},$$

where μ_M is the extinction coefficient as measured and μ_{DW} is the extinction coefficient of the distilled water used in the comparison tube of the photometer. When our paper on under-water illumination in the Tamar Estuary was prepared (Cooper & Milne, 1938), we knew of no modern data on the extinction coefficient of distilled water in the deep red, except those of Lange & Schusterius (1932) which we unjustifiably rejected. James (1938) has since published exhaustive data of his own and gives, in full, results obtained by Prof. J. R. Collins and Dr Ernst Ganz. These leave no doubt that between 700 and 760 mμ the coefficient rises very steeply from about 0·6 to 2·6, and that the distilled water correction which we applied to our results was in serious error. This spectral region is also one in which visual sensitivity is decreasing rapidly. These two factors much favour the transmission and visual perception of light of shorter wave-length. However, the two red filters, S 72 and S 75, equally strongly favour the transmission of light of longer wave-length. Average extinction coefficients cannot be evaluated by simple inspection. Using the data of James, of Collins and of Ganz we have worked them out for the conditions of our experiments.

EFFECTIVE EXTINCTION COEFFICIENT OF DISTILLED WATER MEASURED BY THE RED FILTERS OF THE PULFRICH PHOTOMETER

Consider a light source of known energy distribution and let J_λ represent the relative energy at a given wave-length. After passing through a filter having a transmission c_λ, the relative energy will be reduced to $c_\lambda J_\lambda$. If V_λ represents relative visibility (i.e. the relation between luminous sensation as perceived by the eye and radiant energy), the visual sensation produced by this transmitted light will be $c_\lambda J_\lambda V_\lambda$. The transmission coefficients of the filters expressed as percentages have been supplied by Messrs Carl Zeiss (cf. Cooper & Milne, 1938, Fig. 1). Relative visibility has been taken from

Smithsonian Physical Tables (1933, 8th revised ed.), Table 346; $c_\lambda J_\lambda V_\lambda$ may be plotted against wave-length, and the area $\int_{\lambda_1}^{\lambda_2} c_\lambda J_\lambda V_\lambda \, d\lambda$ enclosed by the curve and the wave-length axis will provide a measure of the light sensation perceived by the observer's eye. It may be evaluated most conveniently with a planimeter.

Since in our work we used 0·25 m. absorption tubes, we have also calculated the relative energy of a narrow wave band, having extinction coefficient μ_λ, after passing through 0·25 m. of distilled water, $J_\lambda e^{-0\cdot25\mu_\lambda}$. This intensity also may be transmitted by the spectral filter and perceived by the eye so that the measure of light sensation will be $c_\lambda J_\lambda e^{-0\cdot25\mu_\lambda} V_\lambda$. This may be plotted on the same graph as $c_\lambda J_\lambda V_\lambda$. The ratio of the areas suffices to evaluate the logarithmic term in the expression

$$0\cdot25\,\mu_A = 2\cdot303 \log_{10} \frac{\int_{\lambda_1}^{\lambda_2} c_\lambda J_\lambda V_\lambda \, d\lambda}{\int_{\lambda_1}^{\lambda_2} c_\lambda J_\lambda e^{-0\cdot25\mu_\lambda} V_\lambda \, d\lambda}.$$

The value obtained for μ_A is the effective extinction coefficient of distilled water for a given filter, which is required as our correction factor. It applies only for 0·25 m. tubes.

Since we do not know the spectral energy distribution of the Nitra lamp supplied with the Pulfrich photometer, we have calculated the effective extinction coefficient, first from Abbot's mean noon sunlight data (Seventh Internat. Congress of Photography, 1929), secondly for light having an equal energy spectrum over the range of wave-length considered, and thirdly for a light source having a colour temperature of 2800° K. (Table I). Considerable latitude in the colour composition of the light source may be tolerated. Much more important are the great variations of the extinction coefficients based on the determinations of different observers and of relative visibility with wave-length. Furthermore, in this region considerable personal idiosyncracy in relative visibility is to be expected.

James (1938, p. 37) discusses the variable coefficients for distilled water found by different observers. These cannot be attributed to errors of measurement and must be due to some variable property of distilled water itself, possibly minute traces of impurities or variable degree of association of the water molecules dependent on the previous history of the water. Whatever the cause, any ordinary laboratory sample of distilled water is likely to show variability at least as great. Below 600 mμ the coefficient is small compared with the measurements on a fairly turbid estuarine water, so that some degree of uncertainty is of little consequence. Above 650 mμ matters are very different. The best we can do is to apply an average effective extinction coefficient as correction factor, as suggested in Table I.

In relatively transparent ocean water, accurate measurement of the extinction coefficients for blue, green and yellow light requires a water column much longer than can conveniently be accommodated by the Pulfrich photometer. Even if this difficulty could be overcome, the correction terms for the absorption of light by ordinary laboratory samples of distilled water remain too uncertain for the method there to be of much value. Its utility is confined to fairly turbid inshore or estuarine waters.

TABLE I. EFFECTIVE EXTINCTION COEFFICIENT FOR RED LIGHT

Transmitted by 0·25 m. of distilled water and measured with the filters of the Pulfrich photometer

	Temperature ° C.	Type of spectrum	Particulars of filters		
Filter no.	...	...	S 75	S 72	S 61
Effective wave-band*, mμ	...	...	730–770	700–760	600–650
Centre of gravity of filter, mμ	...	...	750	729	619
			Effective extinction coefficient		
Calculated from data of:					
James (1938)	Room	Colour temperature 2800° K.	2·24	1·74	...
,,	,,	Equal energy	2·23	1·78	0·28
,,	,,	Mean noon sunlight	2·29	1·76	...
Collins (cit. James)	0·5	,, ,,	2·61	2·02	0·29†
,, ,,	26	,, ,,	2·79	2·14	...
Ganz (cit. James)	12	,, ,,	2·54	1·55	...
Values adopted as correction terms			2·5	1·8	0·28

* These are the limits within which the transmission exceeds one-half the maximum. For purposes of summation, transmissions exceeding one-tenth were included.

† Approximate value obtained by inspection (strictly for equal energy spectrum).

REVISION OF THE ORIGINAL DATA

A list of the numerical revisions made necessary by the change in our correction factors will be found at the end.

The revised values of the ratio μ_λ/μ_{470} for the S 61, S 72 and S 75 filters still show that very turbid waters transmitted red light as well as or better than blue. When μ_λ is graphed against μ_{470}, the relationship may be expressed surprisingly well by the linear equations given in Table II. The constant terms for the red filters are almost the same as those applied to correct for the absorption by distilled water. For the remaining filters similar terms would be quite small. The views expressed in the earlier paper as to the transmission of red light still apply up to about 680 or 700 mμ. Above this the molecules of water itself manifest strong absorption of light, and in fairly clear waters this is all important, but that part of the extinction coefficient, which was due to dissolved and suspended solids, was always least in the deep red. These factors work in opposition, and as a result the minimum extinction coefficient or maximum transmission for our more turbid waters was to be found around 600 mμ.

The ratios of the wave-length at the centre of gravity of the blue S 47 filter compared with the corresponding wave-lengths of the other filters, also given in Table II, show that that part of the extinction coefficient due to suspensoids and possibly to matter in solution is inversely proportional to the first power of the wave-length. The relationship is sufficiently close that, if only one extinction coefficient were known, that for any other wave-length could be calculated with an accuracy sufficient for most practical purposes.

TABLE II. RELATION BETWEEN EXTINCTION COEFFICIENTS AND WAVE-LENGTH

(Revision of original Table III)

Filter	Equation connecting μ and μ_{463}	Ratio of wave-length of blue filter to that of the others (at centres of gravity) $\frac{463}{\lambda}$
S 43	$\mu_{434}=1{\cdot}11\,\mu_{463}$	1·07
S 47	$\mu_{463}=1{\cdot}00\,\mu_{463}$	1·00
S 50	$\mu_{494}=0{\cdot}92\,\mu_{463}$	0·94
S 53	$\mu_{530}=0{\cdot}86\,\mu_{463}$	0·87
S 57	$\mu_{572}=0{\cdot}82\,\mu_{463}$	0·81
S 61	$\mu_{619}=0{\cdot}35+0{\cdot}73\,\mu_{463}$	0·75
S 72	$\mu_{729}=1{\cdot}80+0{\cdot}68\,\mu_{463}$	0·64
S 75	$\mu_{750}=2{\cdot}54+0{\cdot}64\,\mu_{463}$	0·62

The absorption index, K, defined by the equation

$$\mu_{SW}-\mu_{DW}=\frac{4\pi K}{\lambda},$$

is a constant for each water; $\mu_{SW}-\mu_{DW}$ is, in effect, a measure of absorption by suspensoids.

The dependence of scattering of light by particles in sea water upon various powers of the wave-length has been discussed by Kalle (1938).

REVISED DATA (COOPER & MILNE, 1938)

P. 510, Table I: Extinction coefficients of distilled water: Accepted values for filters S 61, S 72 and S 75 are 0·28, 1·8 and 2·5 respectively.

P. 514, l. 26: *For* "($\mu_{500}=5{\cdot}0$; $\mu_{720}=3{\cdot}8$)" *read* "($\mu_{500}=5{\cdot}0$; $\mu_{720}=5{\cdot}3$)".

P. 514, Table II: For last line of figures, read:

μ_{720} 5·9 8·2 7·5

P. 515, ll. 1 and 2 from bottom: *Read:* "the intensity of red and blue light entering the water was cut down to one-thousandth within 0·5 and 0·6 m. respectively ($\mu = 13{\cdot}5$ and 16·5)."

P. 516, Fig. 3: The plots at 610, 720 and 750 mμ should be 0·1, 1·3 and 2·0 units higher respectively. A minimum extinction coefficient occurs at about 600 mμ in most cases.

P. 517, Table III: See p. 394.

Pp. 519 and 520, Figs. 4 and 5: All curves should show less relative energy in the dark red. The statement about preferential transmission of red light does not apply above about 680 mμ.

P. 522, Table IV.

DEPTH IN METRES AT WHICH INTENSITY OF RED LIGHT IS REDUCED TO 1 % OF THAT INCIDENT ON THE SURFACE

Assuming 15 % Surface Loss; $\mu d_1 = 4{\cdot}44$

Centre of gravity of filter mμ	Breakwater No. 1 Buoy	Drake's Island No. 1 Buoy	Hamoaze No. 1 Buoy	Hamoaze No. 7 Buoy	Hamoaze No. 15 Buoy	Neal Point Buoy
		February 18 1937. Spring tide. High water				
619	2·35	1·97	1·85	1·41	1·30	...
729	1·37	1·26	1·22	1·02	0·99	...
750	1·09	1·00	1·04	0·86	0·82	...
		February 16 1937. Spring tide. Low water				
619	1·93	1·95	1·10	0·78	0·53	0·35
729	1·33	1·25	0·89	0·69	0·48	0·33
750	1·04	1·07	0·76	0·60	0·46	0·35
		June 17 1937. Neap tide. High water				
619	3·86	4·27	3·06	2·48	2·54	2·48
729	1·77	1·78	1·60	1·42	1·40	1·39
750	1·38	1·40	1·27	1·18	1·19	1·15
		June 23 1937. Spring tide. Low water				
619	5·00	3·21	2·74	2·04	1·41	0·98
729	1·95	1·60	1·48	1·27	1·00	0·79
750	1·49	1·27	1·16	1·05	0·90	0·71

P. 525, Table V.

DAYLIGHT FACTORS AT BOUNDARIES OF ALGAL ZONES ON BUOYS

No correction for surface loss

	Zone I		Zone II	
	Plymouth Sound	Hamoaze No. 7 Buoy	Plymouth Sound	Hamoaze No. 7 Buoy
Depth of bottom of zone, m. ...	0·18	0·097	0·356	0·223
Daylight factor, %:				
June 17 (high water)	78·3	80·0	62·3	61·8
June 23 (low water)	76·4	77·8	59·2	56·5
February 18 (high water)	65·4	69·8	43·7	45·0
February 16 (low water)	60·9	52·4	37·7	23·3

TABLE VI. DAYLIGHT FACTORS AT BOTTOM OF TWO BUOYS (WITHIN ZONE III)

	Mallard Buoy (Plymouth Sound)			Hamoaze No. 7 Buoy		
Date and state of tide	Depth of bottom of buoy m.	Daylight factor %	Wave-length of maximum transmission mμ	Depth of bottom of buoy m.	Daylight factor %	Wave-length of maximum transmission mμ
June 17 (high water)	2·19	7·41	570	2·47	0·97	570
June 23 (low water)	2·19	5·51	570	2·47	0·35	600
February 18 (high water)	2·19	0·85	580	2·47	0·020	600
February 16 (low water)	2·19	0·34	620	2·47	0·000025	620

P. 524, Table VII. All the extinction coefficients given in the last column should be increased by 1·3.

P. 526, l. 3: *For* "0·36 and 17 m. (ratio 1 : 48)" *read* "0·33 and 17 m. (ratio 1 : 52)."

P. 526, Table in Summary: The values for red light (610–640 and 710–760 mμ) should be increased by 0·1 and 1·33 respectively.

SUMMARY

New values for the extinction coefficient of red light in distilled water require that published results for this coefficient in waters from the Tamar Estuary shall be increased by 0·1, 1·3 and 2·0 at 610, 720 and 750 mμ respectively. Earlier deductions as to the favourable transmission of red light in turbid estuarine waters apply only up to about 680 mμ. That part of the extinction coefficient due to suspensoids and colouring matter was inversely proportional to the first power of the wave-length. Other conclusions remain unaffected.

REFERENCES

COOPER, L. H. N. & MILNE, A., 1938. The ecology of the Tamar Estuary. II. Underwater illumination. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 509–28.

JAMES, H. R., with BIRGE, E. A., 1938. A laboratory study of the absorption of light by lake waters. *Trans. Wisconsin Acad. Sci.*, Vol. XXXI, Chapter II.

KALLE, K., 1938. Zum Problem der Meereswasserfarbe. *Ann. Hydrogr. Marit. Meteorol.*, pp. 1–13.

LANGE, B. & SCHUSTERIUS, C., 1932. Die Absorption des Wassers im sichtbaren Spektralgebiet. *Zeits. Physikal. Chem.*, Abt. A, Bd. 159, pp. 303–5; Berichtigung, *ibid.*, Bd. 160, Heft 6.

THE PLANKTON IN THE UPPER REACHES OF THE BRISTOL CHANNEL

By Colin B. Rees, B.Sc.
University College of Hull Oceanographic Laboratory, Leith

(Text-figs. 1–13)

CONTENTS

	PAGE
Introduction	397
The Station	398
The physical and chemical factors	400
Salinity	400
Temperature	402
pH	402
Phosphates	402
Dissolved oxygen	403
Opacity	403
The bacteria	404
The plankton	405
Diatoms	406
Copepods	411
Other organisms	415
Discussion	415
Acknowledgements	423
Summary	423
References	424

INTRODUCTION

The work embodied in this report was aimed, in conjunction with shore work, at determining the causes of the poverty of the marine fauna and flora in the Cardiff area. The plankton observations were made at a station which was visited 36 times between September 6 1936 and August 25 1937, with an unavoidable absence of visits in October. In addition some results obtained in September 1937 are used.

In so far as the area can be considered as estuarine, this work serves to fill a gap in annual quantitative data for British estuaries. Meek (1923*a*) has dealt with some isolated tow-nettings from the Tyne estuary and, later, Jorgensen (1929) made a more intensive investigation in the same estuary, but did not begin observations until May, thus missing the winter and spring conditions. The Tees survey (Alexander, Southgate & Bassindale, 1935) included counts of *Eurytemora*, marine copepods and *Coscinodiscus*, but variations throughout the year are not noted. Wells (1938) investigated the plankton of the Thames estuary over a number of years. This work, also, was mainly qualitative.

Area 12 of the plankton survey, from 1902 to 1908, of the International Council (Ostenfeld, 1931) was concerned with the Bristol Channel, but the investigations were conducted well outside the present area.

THE STATION

Although it was presumed that the channel in the vicinity of Cardiff had estuarine characteristics, it was decided to restrict observations to one station, and the Cardiff Roads, shown in Fig. 1, was selected. This was largely a matter of convenience, since work was done from a hired motor boat moored at the mouth of the river Ely, and the Cardiff Roads is the nearest place where the depth at high water exceeds 5 fathoms. The position is also sheltered from the prevailing westerly winds so that surface conditions are usually suitable for working there. Since, however, the boat was moored at the mouth of the river, it was very inconvenient to approach the station at low water, and it was owing to this difficulty that the low-water observations are so scanty. This work, therefore, is mainly concerned with high-water conditions.

The Cardiff Roads are about 1¼ miles from the coast, 2 miles from the mouth of the nearest river, the Ely, over 2½ miles from the mouth of the Taff, and 4 miles from the Rhymney. From a width of 13 miles across at Barry, the Bristol Channel suddenly narrows to 8 miles across at the level of the station, and retains this width until near Newport. From Newport there is a further narrowing to the Severn river.

On the up-channel side of the station there is an entry of a large bulk of fresh water derived from the watersheds of the three rivers close to the station, the more distant rivers, the Usk, Wye, Severn, Avon, and a number of smaller rivers. This implies that the station is placed in a buffer area between the sea water of down-channel and the fresh water entering on the up-channel side. Much of the biology of the plankton is dependent on this fact and the relative effect of these bodies of water.

To the narrowing of the channel must be attributed the speed of the tidal streams. At spring tides the stream moves at a normal maximum of 4½ knots in the centre of the channel but may reach higher speeds, and, at neap tides, about 2 knots. The narrowing also affects the height of the tide, causing a spring rise for Penarth, which is probably closely comparable to the station, of 37¾ ft., and a neap rise of 27¾ ft. Tide tables are published in nautical almanacs giving the height of the tide for Penarth, and these values have been used in considering the results obtained.

Since the speed of the tidal streams decreases from the centre of the channel to the coast, no figures can be given for the speeds affecting the investigated area. If, however, we allow that the maximum speed of the tidal stream in the investigated area at neap tide is 1 knot, then the total drift of water within the tidal stream that forms a high tide at the station is 3·86 nautical miles. At spring tide, with a presumed maximum of 2½ knots, the

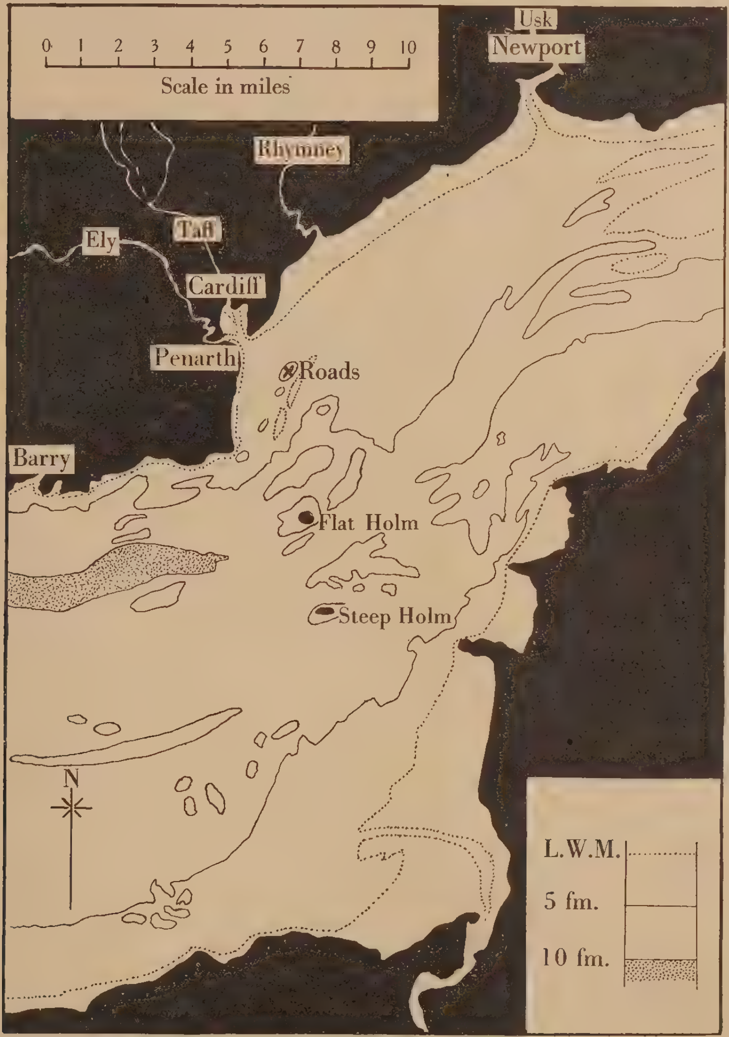

0 1 2 3 4 5 6 7 8 9 10
Scale in miles
Usk
Newport
Rhymney
Taff
Ely
Cardiff
Penarth
Roads
Barry
Flat Holm
Steep Holm
N
L.W.M.
5 fm.
10 fm.

Fig. 1. The upper reaches of the Bristol Channel. The station worked is marked ×.

total drift is 9·66 nautical miles, giving a difference of approximately 6 miles. With speeds of 1 and 2 knots the difference is about 4 miles. Since observations were made at the station at various phases of the tide, the records on different occasions refer, in reality, not to one point, but to a series of points along a length of channel of the order of about 4 miles. On any occasion, the particular point investigated can be defined in relation to the points on other occasions by the height of the tide, i.e. the higher the tide the farther down-channel is the point from which water has come to form a high tide at the station. Having recognized this meaning of height of tide, it becomes clear that a factor which has a direct correlation with the height of the tide must have an increasing value from up-channel to down-channel, and a factor with an inverse correlation must have a decreasing value. These remarks should render what follows more readily explicable.

A number of soundings at the station gave an average depth of about 13 m.

THE PHYSICAL AND CHEMICAL FACTORS

Coincident with the tow-nettings, water samples were taken at the station, transferred in pressure bottles to the laboratory, and analysed within 2 or 3 hr. of collecting. Table I gives the average values of some factors for each month for the surface water at high tide.

TABLE I. AVERAGE VALUES PER MONTH OF HIGH-TIDE SURFACE WATER

Month	No. of samples	Salinity $^{0}/_{00}$	*p*H	P_2O_5 mg. per $m.^3$	Dissolved oxygen c.c.	Temp. of water °C.
Sept.	3	27·1	8·10	69	5·51	17·6
Nov.	2	26·3	7·85	85	5·76	10·1
Dec.	2	25·8	7·90	72	6·66	7·7
Jan.	3	22·5	7·95	55	7·13	7·4
Feb.	2	22·3	7·80	54	7·47	6·4
March	4	22·9	8·00	33	7·19	5·8
April	3	25·4	7·95	44	6·70	9·0
May	4	25·2	8·00	35	6·21	13·0
June	5	26·3	8·05	33	5·80	16·0
July	5	27·3	8·05	36	5·36	17·1
Aug.	3	27·8	8·10	36	5·36	18·9

Salinity. The salinity was determined by titration with silver nitrate.

The average salinity values (Table I) show a steady decrease from September to a minimum in February, followed by a steady rise, except for a slight deviation in May, up to August. This change in salinity demonstrates the effect of the fresh water coming down from the rivers, an effect which must be cumulative and persistent over a period of time.

The minimum value of 19·8 $^{0}/_{00}$ was obtained on January 25, and the maximum of 28·0 $^{0}/_{00}$ on August 25. Fig. 2 shows the changes in value throughout the year. This curve, compared with the curve for the height of tide, shows a well-marked direct correlation between the two factors. That such a correlation exists implies that the bulk of fresh water entering the channel is slow, as well as cumulative, in effect, otherwise variations in rainfall between two successive samples would disturb the correlation.

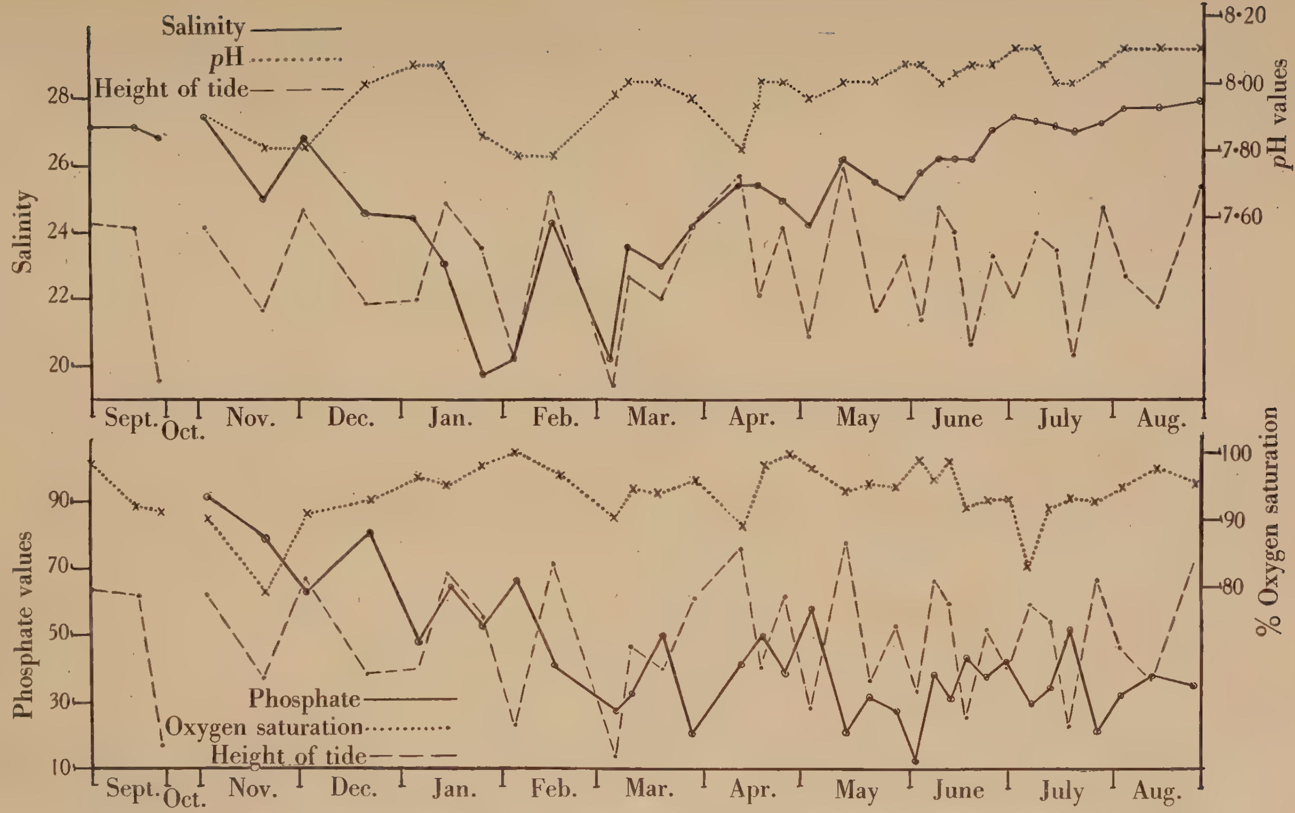


Fig. 2. The relation between the height of tide and the values of salinity, *p*H, percentage oxygen saturation and phosphate for samples taken at the surface at high water.

Water samples were taken on several occasions at various depths from the surface to the bottom by means of the Matthew's Fishery Water Bottle.* Except for one occasion there was no gradient in salinity. The exception was on July 27 (Table II), but this stratification was probably the result of the very heavy rain that fell over a wide area on July 15. A comparison of the weekly rainfall at Ross-on-Wye (*Meteorological Office Report*; Weekly Weather Records) with the changes in salinity suggests that the rainfall in the Wye and Severn catchment areas is effective at the station some 10–14 days after the fall.

TABLE II. SALINITIES $^0/_{00}$ AND SURFACE TEMPERATURE ON JULY 27

High water: 10.20 a.m., 10.23 p.m.; low water: 4.15 p.m.

Time	10.20 a.m.	1.5 p.m.	4.20 p.m.	6.15 p.m.	7.0 p.m.	10.10 p.m.
Surface	27·3	26·7	25·6	26·5	27·2	27·4
4 m.	27·6	26·8	25·9	..	..	28·0
8 m.	28·0	..	25·9	..	..	28·2
12 m.	28·0	..	..	..	..	28·3
Temp. ° C.	17·5	17·2	17·0	17·0	16·9	16·8

Temperature. The temperature readings are correct to 0·1° C. The determined annual range was from 5·2° C. on March 10 to 19·3° C. on August 13. Diurnal variations were small. Table II gives the variation with time and state of tide on July 27. Since this day was colder than the average for the month this range is probably greater than normal.

pH. The *p*H was determined by McClendon's (1917) method with cresol red as indicator.

Since it was found too inconvenient to evaluate the *p*H of the sample immediately, the delay of at least 1 hr. may have caused a change in the value. In addition to this, the salinity varied substantially from time to time, so that readings were made and corrected to an accuracy of *p*H 0·05 only.

The values ranged from *p*H 8·1, which is comparable to normal sea water, to *p*H 7·80. Table I makes it clear that the *p*H change did not follow the salinity change, although the maximum and minimum average values of both occurred in the same month. The change from time to time, as shown in Fig. 2, was erratic, and, unlike the other three factors in this figure, bears no relation to the height of the tide. It is, however, possible that this lack of correlation, over short periods of time, is due to the degree of accuracy being insufficiently fine.

Phosphates. The phosphates were estimated by Atkins' (1923) modification of Denigès' method and the values calculated to milligrams of P_2O_5 per cu. m.

Table I shows that the phosphate values were high up to February, dropped suddenly to 33 mg. in March, and remained about this level until the end of the period. Some of the phosphate that enters the channel as sewage may be precipitated as ferric phosphate. The mud at low water between the Rhymney and Newport contains 4–5 % of iron in its dry weight.

---

* I am indebted to the authorities of the Plymouth Marine Laboratory for the loan of this instrument.

The determined range was from 90 mg. per cu. m. on November 3 to 12 mg. on June 3. Fig. 2 shows the changes throughout the year and further shows that these changes have an inverse correlation with the height of the tide. At the beginning of the period the inverse correlation is not good, but this is probably due to the greater intervals between successive samples during this period. From February onwards the inverse correlation is good, the biggest deviation being the lowest value of 12 mg. on June 3.

The values given in Table III for the change of phosphate value with the state of the tide on July 27 show that there was a higher concentration of phosphate at low water than at high water.

TABLE III. CHANGES OF PHOSPHATE AND OXYGEN SATURATION WITH STATE OF TIDE ON JULY 27

	High water	Low water	High water
Phosphate	22	37	22
Oxygen saturation	93	87	92

Dissolved Oxygen. The oxygen content was determined by Winkler's titration method, and the values for percentage oxygen saturation calculated from Fox's (1907) tables. The precaution advised by Alsterburg (1926) of not permitting the sample, after adding the Winkler's reagents, to stand for more than 15 min. before acidifying, was adopted. This precaution minimizes possible errors due to organic matter and ferric ions.

The determined range for high water was from 5·26 c.c. per l. on August 25 to 7·78 c.c. on February 4. The percentage saturation range was from 79% on November 20 to 100% on February 4 and April 25. This value of 79% must be regarded as exceptional, since the oxygen saturation value was over 90% in 35 out of 38 samples taken at high water. This implies that the oxygen saturation is more a function of temperature and salinity than of any other factors. In Fig. 2 the changes in percentage oxygen saturation are shown, and, though by no means well marked, there is an apparent inverse correlation with the height of tide.

Table III shows that on July 27 the oxygen saturation was less at low water than at high water, and other samples taken at low water have a lower oxygen saturation than is general for high-water samples.

Opacity. The amount of suspended matter was considerable. A Secchi's disk of 9 in. diameter became invisible at depths of little more than 0·5 m. at high water. This is approximately the same as in the Tees estuary (Alexander *et al.* 1935) at the same salinity. However, the value of 0·5 m. is a generous one, since the readings were made at slack water on calm days. As a result of the gradual deposition of silt under such conditions the water becomes clearer. With the beginning of the tidal stream the silt is again stirred up, and a swell, even at slack water, prevents deposition.

The water is more opaque at low water than at high water and, as on July 27, a pronounced change in opacity may occur about mid-water flood.

Note must be made of the substantial quantities of coal dust present, as indicated in the tow-nettings. Usually its presence was more clearly marked in the deep hauls, but it was occasionally found in the surface hauls. This depended on the state of the water.

THE BACTERIA

From February to August 1937 nine samples of sea water were taken at the station, and the bacteria investigated to a limited extent. All the samples were taken at high water. The procedure adopted was, as nearly as possible under the conditions of working, that recommended by the Ministry of Health (1936).

The examinations made were:

(*a*) Agar count at 20° C. (room temperature), Table IV.
(*b*) Agar count at 37° C.
(*c*) *Coli-aerogenes* count.

TABLE IV COLONIES DEVELOPING AT ROOM TEMPERATURE

Date	0·5 c.c.	0·5 c.c.	0·1 c.c.	0·1 c.c.	Total	Average per c.c.
Feb. 15	209	183	..	..	392	392
Mar. 6	238	208	45	..	491	446
April 11	340	290	..	..	630	630
May 13	321	..	60	69	450	643
June 3	95	..	27	18	140	200
July 7	168	175	56	52	451	376
July 19	115	112	15	13	255	213
Aug. 25	129	..	27	33	189	270
	Total number of colonies counted				2998	
	Average per c.c. determined for the period					396

Owing to the spreading over of the plates by sporing organisms, the counts of colonies developing at 37° C. (Table V) are generally minimum. A number of the incubated plates were rendered useless and were discarded. As, frequently, the whole batch of plates was affected, counts were made of the better plates as long after 24 hr. and as near to 48 hr. as possible. The counts on July 7 and August 25 were of good plates incubated for the full 48 hr., and it is seen that these give quite the highest numbers of the series.

TABLE V. COLONIES DEVELOPING AT 37° C.

Date	1 c.c.	1 c.c.	0·5 c.c.	0·5 c.c.	Total	Average per c.c.
Feb. 15	24	..	15	..	39	26
Mar. 6	84	69	..	..	153	76
Mar. 10	58	53	33	..	144	58
April 11	..	..	29	23	52	52
May 13	..	..	..	32	32	64
June 3	..	..	18	16	34	34
July 7	..	..	94	..	94	188
July 19	..	..	47	50	97	97
Aug. 25	..	..	67	76	143	143
	Total number of colonies counted				788	
	Average per c.c.					72

The *coli-aerogenes* counts (Table VI) were obtained by inoculating the sea water and dilutions of it, made by adding the sample to sterilized tap water, into tubes of MacConkey broth. The tubes were incubated for 1 or 2 days, and, from the number of tubes giving a positive reaction for acid and gas, the probable number of *coli-aerogenes* colonies in the initial sample was obtained by reference to McGrady's tables (see Ministry of Health, 1936). The numbers obtained were so high that it was considered unnecessary to distinguish between *Bact. coli* and *Bact. aerogenes*, especially as there are several intermediate types.

TABLE VI. COLONIES DEVELOPING IN MACCONKEY BROTH

Quantity of sample in each tube ..	10 c.c.	1 c.c.	0·1 c.c.	0·01 c.c.	Probable no. of colonies per 100 c.c.
No. of tubes used ..	5	5	5	5	
Date	No. of tubes giving positive reactions				
Feb. 15	5	5	4	..	1600
Mar. 6	5	5	4	3	1600
Mar. 10	..	5	3	..	900
April 11	..	5	4	1	1600
May 13	..	5	5	3	1800 +
June 3	..	2	0	..	..
July 7	..	5	3	..	900
July 19	..	5	4	1	1600
Aug. 25	..	5	5	2	1800 +

The counts given in Tables V and VI, particularly in the latter, indicate a measure of sewage pollution.

Comparative results are given by Meek (1923 *b*) for the Tyne estuary. On agar incubated at 37° C. 1000 colonies per c.c. were recorded for March, increasing to 2400 in May. *Bact. coli* remained constant at about 100 per c.c. throughout. These numbers are very much higher than those for the plankton station. Lloyd (1930), on the other hand, found lower numbers of colonies developing at room temperature in the surface water in the Clyde Sea area, even in the heavily polluted Greenock and Cumbrae Deep areas. However, in making strict comparison between the three sets of results, the influence of differences of technique on the numbers obtained has to be kept in mind. In this connexion the recent work of Dianova & Voroshilova (1935) on the salt composition of the medium and the specificity of marine bacteria is important.

THE PLANKTON

All the tow-nettings were made with a conical tow-net with a mouth 0·5 m. in diameter and silk of 100 meshes to the inch. The net was towed horizontally for 20 min. at the surface, and at times for 10 min. at a depth of 2–4 m. from the bottom. Particular attention was paid to the surface hauls which were fully analysed quantitatively, but, owing to the greater amount of detritus, the deep hauls could not be treated in such detail. The method of counting was rigorously standardized from the beginning, counts being made in a subsample on a ruled slide. The subsample consisted of 0·5 c.c. and was removed while the plankton sample was being shaken. At least two counts were made. If the difference in the two counts was more than 10% further counts were made until two counts gave such consistency; usually, however, two counts were sufficient.

Table VII gives the distribution of the tow-nettings for each month. A few of these were taken at night, but, as there was no perceptible difference between night and day hauls, they are not specifically noted.

TABLE VII. DISTRIBUTION OF TOW-NETTINGS IN EACH MONTH

		Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Total
High water:	Surface	3	2	2	3	2	4	3	3	5	6	3	36
	Deep	2	2	2	3	1	3	2	1	.	.	.	16
Low water:	Surface	.	1	1	.	.	.	.	.	.	1	.	3
	Deep	.	1	1	.	.	.	.	.	.	.	.	2
Other tow-nettings		.	.	.	.	.	.	.	.	.	2	2	4
											Total examined		61

Table XII gives a list of the species identified and the average numbers in the high-water surface counts for each month, except when otherwise noted. This list is not complete, some species present in very small numbers being omitted. Only numbers of 1000 or more for diatoms, and 500 or more for copepods and larval forms, are considered significant, and other numbers are not shown except when the maximum number obtained is given as an indication of frequency and seasonal distribution.

Diatoms

Twenty-four species of diatoms (Table XII) have been identified and all these, except the estuarine species *Nitzschia sigma* W.Sm.,* are typically marine. The bulk of the diatoms collected consisted of *Biddulphia sinensis* Grev., *Rhizosolenia setigera* Brightw., *Biddulphia regia* M. Schultze and *Bacillaria paradoxa* Gmel. Next in importance came *Streptotheca thamensis* Shrubs., but even though increasing to the end of the period, it was throughout overshadowed by the numbers of the four main diatoms. Centrifuged samples indicated that *Skeletonema costatum* (Greville) and small *Coscinodiscus* species were the most frequent diatoms in the summer and not the diatoms caught by the tow-net. This is to be expected from the collecting method used, and it is to be understood that the present account of the diatoms in this area is virtually reduced to a consideration of four species only.

The average total diatom counts for each month are given in Table VIII and Fig. 3. From these it is apparent that the maximum number occurred in November, and the minimum in April. These numbers are, however, not particularly instructive. From the middle of November onwards *Biddulphia sinensis* gradually decreased in numbers and yet it made up more than 50%

* I am indebted to Dr M. V. Lebour for confirming this identification.

of the samples until the beginning of May. This decline, therefore, obscures the changes in numbers of the other diatoms. Table VIII and Fig. 4 give the average numbers of all diatoms counted, with the exception of *B. sinensis*. These showed a minimum in December with a steady rise to the highest number in August. The steadiness of this rise is noteworthy. Except between January and February the diatom numbers are not doubled from one month to the next.

By comparing the two numbers for each month in Table VIII it can also be seen that the samples in August 1937 were very different in composition from those in September and especially November 1936. The tow-netting taken at the end of September 1937 still showed this difference. In the beginning of the period *B. sinensis* made up practically the whole of the samples, while at the end of the period it was relatively unimportant. The proportion *B. sinensis* to other diatoms changed from 7 : 2 in September and 34 : 1 in November to 1 : 26 in August.

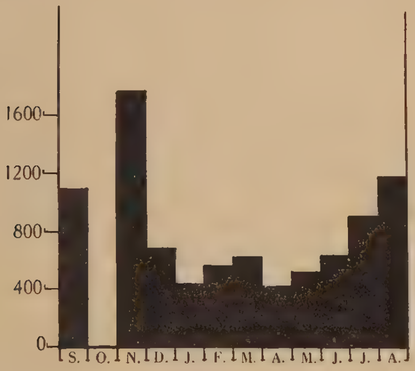


Fig. 3.

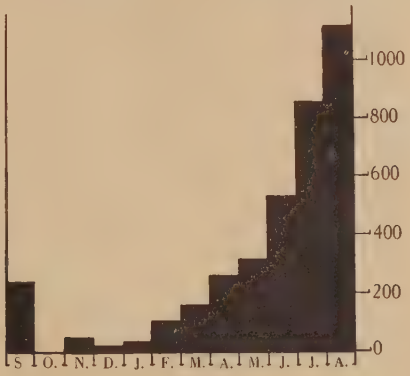


Fig. 4.

Fig. 3. The average numbers per month of all the diatoms counted in the tow-nettings. (No observations in October.)

Fig. 4. The average numbers for each month of all the diatoms except *Biddulphia sinensis* in the tow-nettings. (No observations in October.)

TABLE VIII. AVERAGE NUMBER OF THOUSANDS OF DIATOMS PER MONTH

	Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Total diatoms	1080	1750	672	432	567	620	420	518	625	900	1170
Total less *Biddulphia sinensis*	240	50	22	32	107	160	260	318	533	860	1127

In Fig. 5 the changes in the values for each of the four main diatoms, expressed as percentages of the total diatoms counted, are related to the height of the tide. A series of values of under 10% for any diatom is considered insignificant.

On the basis of the information in this figure, the period of survey can conveniently be divided into four periods.

September 19–February 4. During this period *B. sinensis* made up more than 90% of the diatom samples. This made the changes in percentage of all other diatoms insignificant and, in addition, made the changes in *B. sinensis* itself insignificant so that this period is not included in Fig. 5.

February 4–April 17. This period is shown in Fig. 5. On February 4 the percentage value of *B. sinensis* was 97% and of *Bacillaria paradoxa* 1%. On February 15 there was a change to 74% and 20%. This is the first stage of a period in which the values of *Biddulphia sinensis* varied inversely, and those of *Bacillaria* varied directly, with the height of the tide.

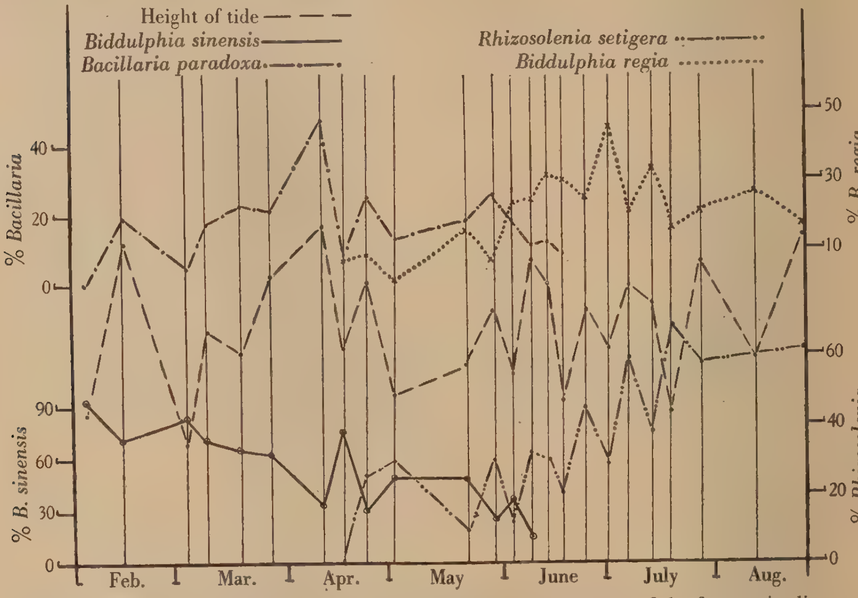


Fig. 5. The relations between the height of tide and the percentage of the four main diatoms to the total diatoms counted in the samples from February 4 to August 25.

April 17–June 18. During this period a transition occurred between the conditions in the last period and the next. *Biddulphia sinensis* and *Bacillaria* were still correlated with the height of the tide, but approached the value of 10% and by June 18 became insignificant. *Rhizosolenia setigera* suddenly jumped from under 1% on April 17 to 25% on April 25. Up to May 21 the values had no distinct relation with the height of the tide, but from that date they were directly correlated. *Biddulphia regia* was insignificant until May 21 (although Fig. 5 includes values from April 25) and from then on was inversely correlated with the height of the tide.

June 18–August 25. During this period only two diatoms were concerned. The percentage values of *Biddulphia regia* continued their inverse relation, and those of *Rhizosolenia setigera* their direct relation with the height of the tide. These correlations are well marked and do not break down until July 19. From then onwards the correlations are indefinite, the values differing little from time to time.

Within the actual total numbers of diatoms there are (Fig. 5) diatoms showing different relations with the height of the tide. Although effective in different periods *Biddulphia sinensis* and *B. regia* agree in being inversely correlated, and *Rhizosolenia* and *Bacillaria* agree in being directly correlated with the height of the tide. In Fig. 6 this distinction is recognized. Here are given the changes in the actual numbers obtained of *Biddulphia sinensis* plus *B. regia*, and the changes in the numbers of the remaining diatoms. In the first of these there is a clear inverse relation with the height of the tide and in the latter a direct relation. The correlations are by no means exact, but since we are dealing with numbers in which enormous variation may occur, owing to the quantitative method used, such a result is to be expected.

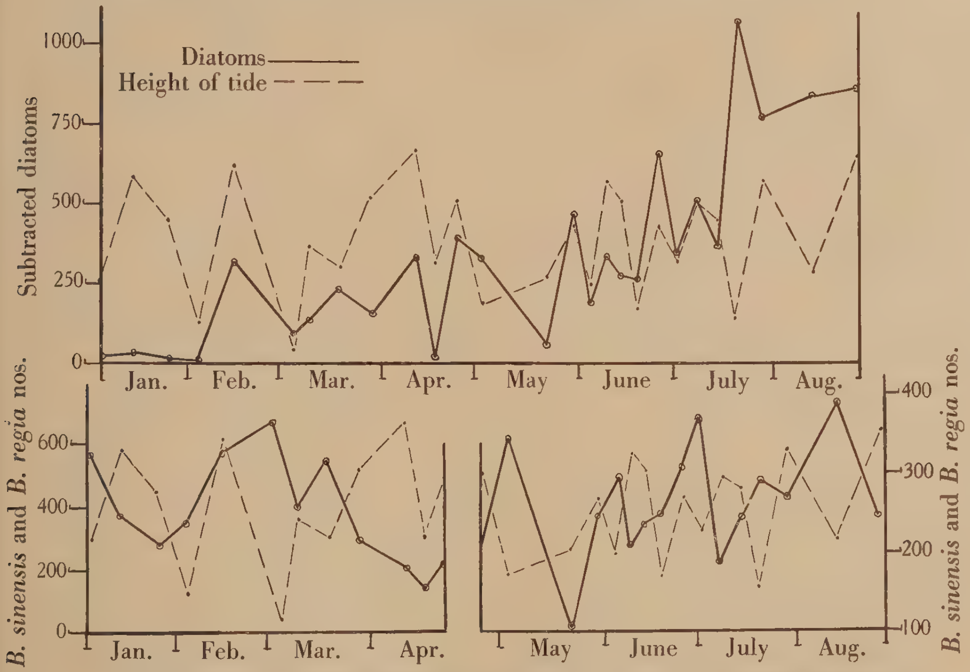


Fig. 6. The relation between the height of the tide and (1) the numbers of *Biddulphia sinensis* plus *B. regia*, (2) the numbers of the remaining diatoms, in the samples from January 5 to August 25.

There is no persistent correlation between the height of the tide and the total number of diatoms, and these correlations become apparent only when a distinction is made between the diatoms according to the information in Fig. 5.

On July 27 five tow-nettings were taken from one high water to the next. Table IX gives the percentage composition of the diatoms in each tow-netting. These values are plotted in Fig. 7 and show that the composition varied considerably between high water and low water. At high water *Rhizosolenia* was dominant and at low water *Biddulphia regia* made up the bulk of the catch. The values for *Bacillaria* and *Biddulphia sinensis* indicate also, in so far as one can accept changes within this range of values, that *Bacillaria* decreased and *Biddulphia sinensis* increased in percentage values at low tide. Care is required in considering these, since the values at high water were conditioned by *Rhizosolenia* and at low water by *Biddulphia regia*.

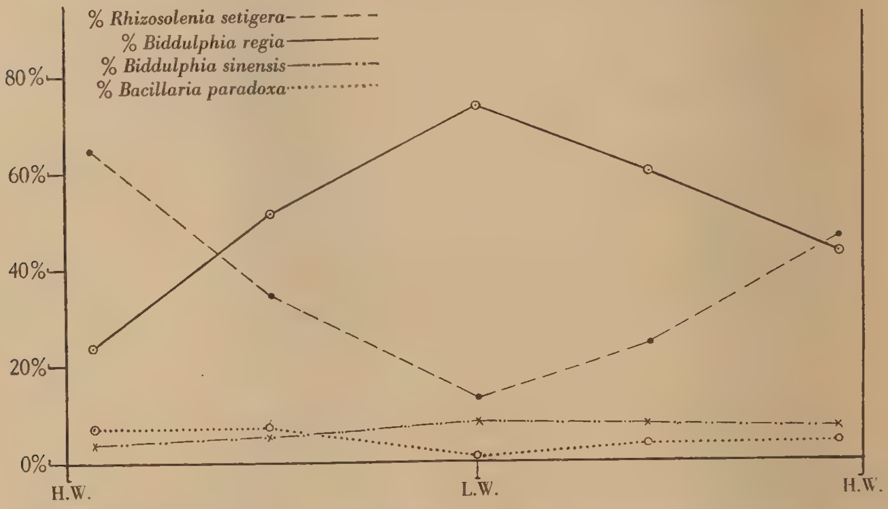


Fig. 7. The changes in the percentage composition of the diatom samples with state of tide on July 27.

TABLE IX. PERCENTAGE COMPOSITION OF DIATOMS ON JULY 27

	Rhizosolenia	*Biddulphia regia*	*Bacillaria*	*Biddulphia sinensis*
High water	65	24	7	4
Mid-water ebb	35	52	8	6
Low water	14	74	2	9
Mid-water flood	25	61	5	9
High water	46	43	5	6

The diatom numbers in each haul are relative only to one another. In order to obtain numbers which could be compared with those from other areas, water samples of 20 c.c. were centrifuged at intervals from the end of April to July and the diatom chains counted. Owing to the considerable quantities of silt there was a limit to the volume of water that could be centrifuged, and, even so, the counts obtained are minimum owing to the masking effect of the deposited silt. The counts were so low, however, that errors are unimportant. The counts varied from 72 diatom chains per 20 c.c. on June 3 to 22 on May 13. Fig. 8 shows an inverse relation between the numbers and the height of the tide. Samples in November gave counts of under 10 diatom chains per 20 c.c. and sometimes there were no diatoms present.

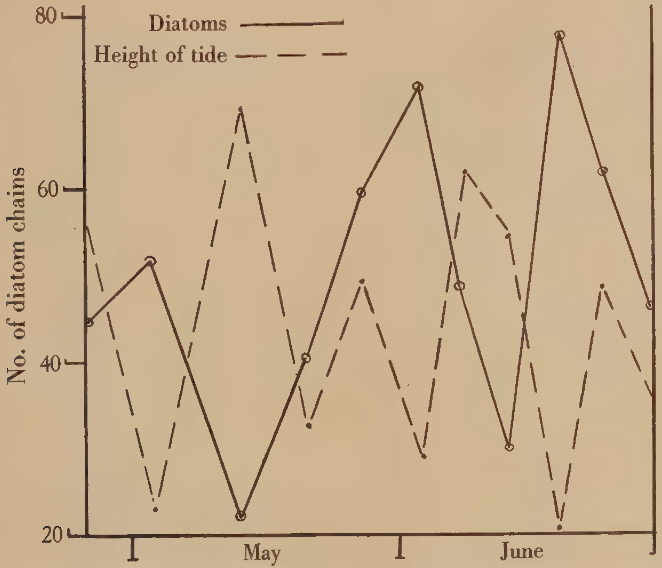


Fig. 8. The relation between the height of tide and the number of diatom chains in 20 c.c. of water from April 25 to July 1.

Copepods

Only eight species of pelagic copepods (Table XII) are recorded from the station, and, of these, five species alone were present in significant numbers. These were, in order of importance, *Eurytemora affinis* (Poppe), *Acartia bifilosa* (Giesbrecht), *Euterpina acutifrons* (Dana), and, of much lesser significance, *Oithona nana* Giesbrecht and *Centropages hamatus* (Lilljeborg). The other species were present sporadically and in small numbers. Fig. 9 presents the seasonal distribution in the numbers of the three main species.

Eurytemora affinis was the most interesting copepod obtained. Variations in numbers from time to time were sufficiently great to represent changes in actual density at the station, rather than changes due to unequal or inefficient sampling by the tow-net. I have followed Gurney (1931) in not separating the form *E. hirundoides* from *E. affinis*. As yet the copepodid stages and adults have not been analysed, and the numbers refer to the total *Eurytemora* irrespective of stage.

While a varying number of specimens were obtained outside this period, *Eurytemora* reached significant numbers, i.e. 500 or over, between November 3 and June 8. The highest average for any month occurred in April (Fig. 9) with over 28,000, and this was closely followed in May with nearly 27,000. The highest number obtained at the surface was 59,000 on May 21, and it is this number which makes the average for May high, since on May 27 a sudden decrease in numbers was obtained (Table X). A further decrease occurred on June 8. The rapidity of this decrease is striking.

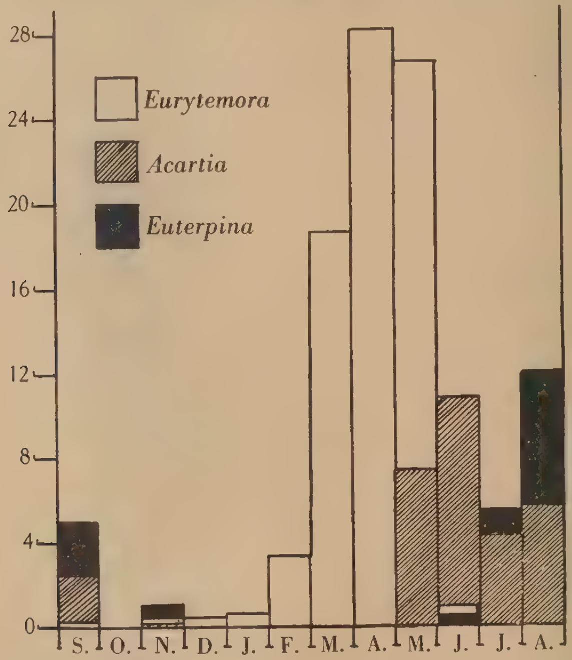


Fig. 9. The average numbers per month of the three chief copepods. (No observations in October.)

Table X. NUMBERS OF *EURYTEMORA* AND *ACARTIA*

Date ..	Apr. 25	May 3	May 21	May 27	June 3	June 8
Eurytemora	32,000	17,000	59,000	3,200	4,800	400
Acartia	..	800	20,000	1,600	25,600	13,200
Height of tide	37 ft. 4 in.	30 ft. 6 in.	32 ft. 4 in.	35 ft. 1 in.	31 ft. 8 in.	38 ft. 5 in.

In Fig. 10 the numbers of *Eurytemora* obtained at the surface are plotted against the height of the tide. Allowing for the sudden drop in numbers on May 27, there appears to be a direct correlation, with a single exception in the coincidence of the form of the curves on April 17. In this figure, also, is plotted the numbers of diatoms caught in the period, and there is, here, an inverse relation between surface *Eurytemora* and diatoms. This is to be expected, since, during this period, *Biddulphia sinensis* made up more than 50% of the diatoms collected and the diatom curve will tend to follow the *B. sinensis* curve, i.e. inverse with the height of the tide.

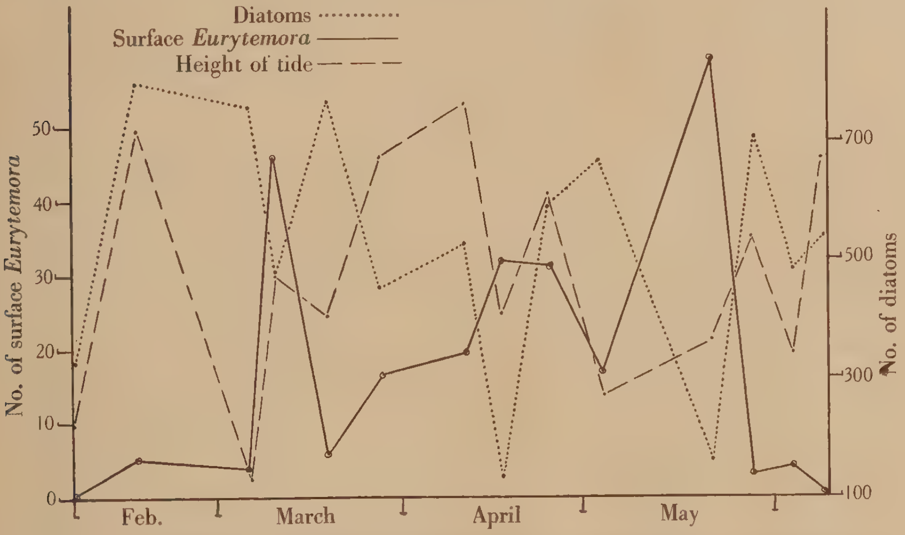


Fig. 10. The relations between the surface *Eurytemora* and (1) height of tide, (2) total diatoms, from February 4 to June 8.

Over a short period quantitative data for *Eurytemora* are available from deep hauls. The numbers obtained were higher than at the surface. On March 6, for example, over a quarter of a million were obtained in 10 min. towing. Since the duration of the bottom hauls was half that of the surface hauls the numbers are here doubled. The total numbers of *Eurytemora* obtained from the surface and the bottom, when both records are available, are plotted in Fig. 11. In contrast to Fig. 10 there is an inverse correlation with the height of the tide. The surface *Eurytemora*, expressed as percentages of the total *Eurytemora* obtained, are also plotted in this figure, and their direct correlation with the height of the tide is well marked.

Acartia bifilosa. This species was present in significant numbers up to November 20 and from May 3 to the end of the survey. Table X shows that, at about the time of the rapid decline in numbers of *Eurytemora*, there was a rapid increase in the numbers of *Acartia*, and also that, during this period, the numbers were inversely correlated with the height of the tide. On no occasion after June 8 were more than 10,000 *Acartia* obtained, so that variation in numbers may well have been due to unequal sampling.

Euterpina acutifrons agreed closely with *Acartia* in time distribution, and was significantly present up to November 27 and from May 27 to the end of the survey. In this species, the rise in numbers to the maximum of 20,000 on August 25 was gradual.

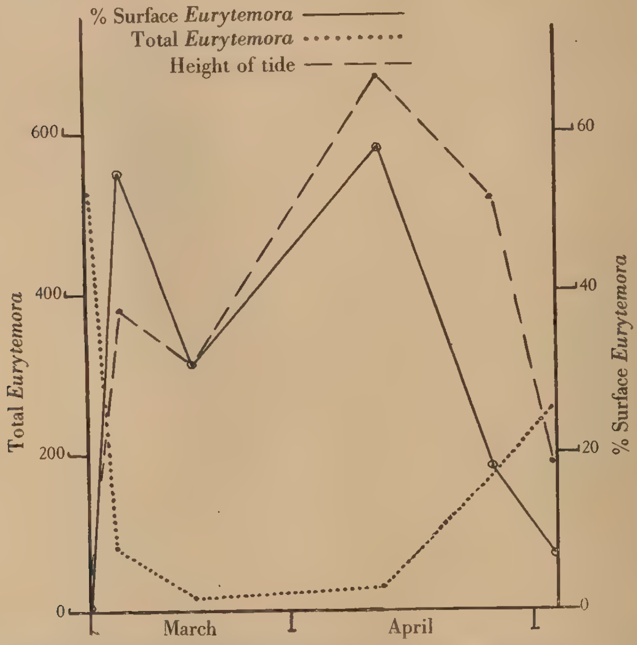


Fig. 11. The relations between the height of tide and (1) total *Eurytemora*, (2) percentage of the total *Eurytemora* at the surface.

Oithona nana was present in significant numbers from September 6 to December 21. Except for a few specimens at the end of the period of survey it did not reappear.

Centropages hamatus was present in significant numbers only in September, though a few specimens were present at the end of the survey.

Table XI gives the percentage distribution of the copepods with the state of the tide on two separate occasions. We see here that *Eurytemora* was quite unimportant at high water, but was the dominant form at low water. *Euterpina* was the most frequent copepod at high water, while *Acartia* appears to maintain an even percentage value, but it must be realized that its value at high tide is determined by *Euterpina* and at low water by *Eurytemora*. *Oithona* was present at one high tide only.

TABLE XI. PERCENTAGE DISTRIBUTION OF COPEPODS WITH STATE OF TIDE

Date	State of tide	*Acartia*	*Eurytemora*	*Euterpina*	*Oithona*
July 27 1937	High water	41	4	55	..
	Low water	40	58	2	..
Sept. 20 1937	Low water	22	58	20	..
	High water	24	..	67	9

The list of harpacticids (Table XII) is not unusual for estuaries or turbulent water. *Tisbe furcata* (Baird) was interesting in that a number of the specimens carried the suctorian *Ophryodendron trinacrium* Grüber.

Other Organisms

The remaining species and larval forms identified are of little interest. As with the diatoms and the copepods, there is a distinct poverty in the number of species. A considerable number of the species listed in Table XII cannot be considered pelagic, and are present in the tow-nettings, as commonly in other estuaries, owing to the turbulence of the water.

As regards the larger Crustacea, the numbers give little indication of their frequency since the tow-net used was too fine to catch good samples of, for example, the mysids. The largest number of mysids taken was 75 at the surface at low water. Usually there were more mysids and amphipods in the deep hauls, but there was no marked difference between day and night hauls.

Of the larval forms, cirripede nauplii were present in greatest numbers, with a maximum in April. The numbers for the polychaete larvae are shown as those of *Nerine*, *Autolytus* and general polychaete larvae. This latter group, during the summer and autumn, consisted mainly of the larvae of *Sabellaria alveolata* Linn. (Wilson, 1929) which is common along the shore and is probably present on the bottom under the plankton station.

Both *Podon polyphemoides* and ascidian tadpoles appeared suddenly on June 18 and had virtually disappeared by June 24.

DISCUSSION

It has already been explained (p. 398) that, because of the varying speeds of the tidal stream, the observations made at the station are referable to a series of points along a length of the channel, and that the points can be related to one another by the height of the tide, i.e. the highest spring tide refers to the farthest point concerned down-channel and the lowest neap tide to the nearest point down-channel, and so on. Therefore the vertical measure of the height of the tide can be used as a horizontal measure of a length of channel. This length will be referred to as the investigated length.

TABLE XII. LIST OF SPECIES AND AVERAGE MONTHLY CATCHES

	Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Diatoms. Nos. refer to thousands											
cMelosira Borreri Greville	..	..	..	..	+	+	+	3*	..	..	..
cParalia sulcata (Ehr.)	+	+	+	1·4	3	5·4	7	3	1·5	+	+
Coscinodiscus Grani Gough	58	4·5	1·2	..	..	..	..	..	..	+	+
Coscinodiscus excentricus Ehr.	+	3	3	7	4	9	11	13	18	7	5
Coscinodiscus radiatus Ehr.	+	3	2	+	1	1	3	4	7	2	+
Actinoptychus undulatus (Bail.)	..	..	+	+	+	2	3	2	4·6	1	+
Actinoptychus splendens (Ehr.)	..	..	..	..	..	+	+	..	..	..	..
cSkeletonema costatum (Greville)	..	..	..	..	+	6	+	9	11	10	4·2
Rhizosolenia setigera Brightw.	14	13	3	4	4·5	4	6	130	190	500	650
cChaetoceros borealis Bailey *cChaetoceros didymis* Ehr.	1	..	..	..	..	..	..	..	4·6	18	2
Biddulphia mobiliensis Grev.	..	..	..	..	6	7·4	9	6	1·6	1	..
Biddulphia regia M. Schultze	57	16	4	1	4·4	11·5	9	30	168	230	210
Biddulphia sinensis Grev.	840	1700	650	400	460	460	160	200	92	40	43
Biddulphia favus (Ehr.)	..	..	..	..	..	+	0·6	+	+	+	..
cBellarochia malleus (Brightw.)	+	+	+	..	..	+	+	0·6*	+	+	+
Dytilium Brightwelli (West)	..	..	..	..	..	..	..	1*	+	2*	..
cStreptotheca thamensis Shrubs.	..	..	..	..	..	1	15	14	36	30	75
cAsterionella japonica Cleve & Möller	+	+	..	..	..	..	..	..	..	0·5	+
cAsterionella kariana Grun	..	..	..	+	+	..	..	+	..	..	..
cThalassiothrix nitzschioides Grun	9·4	4	1	2	0·7	1·5	1	+	+	+	+
Gyrosigma sp. Hassal	..	+	+	..	..	+	..	..	..	..	..
cBacillaria paradoxa Gmel.	28	21	10	7	85	80	140	100	70	60	76
Nitzschia sigma W. Sm.	2	3	3·7	3	1·5	3·5	1	+	2	1	1
Other phytoplankton organisms. Nos. refer to thousands											
Ceratium furca (Ehrenberg)	+	..	..	1*	..	+	0·7*	+	+	+	+
Halosphaera viridis Schmitz	..	..	..	..	+	1	1·6	2	+	..	..
Copepods. Nos. refer to hundreds											
Calanus finmarchicus (Gunnerus)	..	..	..	..	0·01*	0·01*	0·01*	..	..	..	..
Pseudocalanus elongatus Boeck	..	..	..	+	+	1*	4*	+	+	..	..
Centropages hamatus (Lillejeborg)	6·5	+	+	..	..	..	..	+	..	+	..
Temora longicornis (O. F. Müller)	..	..	+	0·02*	+	..	..	..	..	..	..
Eurytemora affinis (Poppe)	+	5	5	6	34	187	284	267	10	+	..
Acartia bifilosa (Giesbrecht)	23	+	..	..	..	..	..	75	109	53	59
Euterpina acutifrons (Dana)	50	10	+	..	..	..	..	+	5	44	120
Oithona nana Giesbrecht	6	+	11	+	+	..	..	..	..	+	..
Cladocera											
Podon polyphemoides Leuck.	..	..	..	..	..	..	..	..	5600*	..	..
Peracarids											
Gastrosaccus spinifer (Göes)	..	..	75*†	7	1	2	2	..	..	..	..
Schistomysis spiritus (Norman)	23	+	4	..	..	1	6	..	1	7	7
Schistomysis ornata (G. O. Sars)	..	..	..	2*	..	..	..	..	..	..	..
Mesopodopsis slabberi (van Ben.)	..	..	..	..	..	..	12	8	21	10	5
Neomysis integer (Leach)	..	..	..	..	..	1*	..	..	..	..	..
Diastylis rathkei (Kröyer)	1*‡	1*‡	..	..	..	..	..	..	..	..	..
Eurydice pulchra Leach	1*	..	..	..	..	..	..	..	..	..	..
Sphaeroma serratum (Fabr.)	..	..	..	1*	..	..	..	..	..	..	..
Notropis swammerdami (H. Milne-Edwards)	..	..	1*	..	..	..	..	..	..	..	..
Gammarus locusta (L.)	1*	..	..	..	..	..	..	..	..	..	..
Gammarellus homari (Fabr.)	..	..	..	12	8	3	..	..	..	..	..
Decapods											
Pandalus montagui Leach	..	3*†	..	1	..	.	..	..	..	..	..
Crangon vulgaris L.	..	1*†	..	..	..	..	..	..	..	..	..
Pasiphaë sivado (Risso)	..	..	..	..	..	..	..	..	..	2*	..
Other zooplankton species											
Foraminifera	800	+	+	..	..	..	..	..	..	..	..
Pleurobrachia pilosa (O. F. Müller)	2	1	..	+	..	..	..	..	16	17	6
Sagitta setosa J. Müller	2	..	..	..	..	..	..	+	3	1	2
Eteone sp.	..	..	..	2*§	..	1*	..	..	..	..	..
Oikopleura dioica Fol.	200	..	..	..	..	..	..	..	300	400	1000
Elvers	..	..	..	..	..	2*	..	..	..	..	..
Larval forms											
Ephyra	..	..	..	..	2*	..	..	..	..	..	..
Cyphonautes	..	+	..	..	..	..	..	..	..	..	..
Echinoplutei	10*	..	..	..	..	..	..	..	..	..	..
Post larval asteroids	10*	..	..	..	..	..	..	..	..	..	..
Larvae of *Nerine*	..	..	..	..	..	1200	900	400	+	..	..
Autolytus larvae	..	..	..	..	..	+	4	+	+	+	..
Polychaete larvae	500	500	+	500	800	3800	1600	2800	6000	7600	4000
Nauplii	..	1000	500	3600	4100	1900	1900	5000	860	1400	1600
Cirripede nauplii	2200	560	..	..	700	12400	16000	8000	10000	7300	2000
Cypris larvae	300	+	..	..	..	..	..	750	+	..	..
Cryponiscid	..	..	..	..	..	+	..	..	..	+	..
Macruran protozoea	..	..	..	..	..	2*	..	..	..	..	..
Megalopa	..	..	..	..	..	..	..	..	..	..	5*
Zoea of *Carcinus maenas*	250	..	..	..	..	..	..	..	..	+	+
Gastropod larvae	550	..	..	..	..	500	+	+	3100	4000	2600
Lamellibranch larvae	200	200	1100	950	200	950	700	300	..	..	..
Ascidian larvae	10*	..	..	..	..	..	..	..	600*	+	..
Ovum hispidum hystrix	..	..	..	..	..	..	..	..	+	700	1400

Harpacticids

Longipedia minor Scott
Canuella perplexa Scott
Ectinosoma curticorne Boeck
Zaus goodsiri Brady

Alteutha interrupta (Goodsir)
Tisbe furcata (Baird)
Tachidius littoralis Poppe
Tachidius discipes Giesbrecht
Macrocheiron fucicolum Brady

* Number in a single tow-netting only.
§ Night tow-netting.
† Low-water haul.
+ Indicates presence.
‡ Bottom haul.
c Numbers refer to chains of diatoms.

Since the higher the tide the farther down-channel is the point involved in investigation, the direct correlation between the salinity and height of tide (Fig. 2) means that there was a gradient of increasing salinity from up-channel to down-channel. Quite apart from this correlation, such a gradient is to be expected, and the existence of the correlation serves as a check on the distinction between observations at a single point and along a length of channel. It also shows that changes in values along the investigated length are sufficiently large to be easily observable. While normal variations in rainfall do not upset this correlation, it is possible, as Prof. Tattersall suggests, that the local influx of fresh water from the Taff and adjacent rivers causes a steeper gradient in the region of the station than farther out in the channel. If this is so the range of values at a station nearer mid-channel would not necessarily be greater than at the present station, in spite of the increase of the investigated length due to greater divergence in the speeds of the spring and neap tidal streams.

The inverse relation between the phosphate values and the height of the tide indicates a gradient of decreasing phosphate. This is further borne out in Table III which shows that phosphate values are higher at low water. Low water observations refer, of course, to a point considerably farther up-channel than the investigated length.

Table III shows, also, that the oxygen saturation was less at low water than at high water, yet Fig. 2 appears to indicate, from the inverse correlation with the height of tide, that there was a decreasing oxygen saturation from up-channel to down-channel. These results are not necessarily inconsistent. Meek (1923*b*) found that the dissolved oxygen content in the Tyne estuary is almost entirely dependent on fresh water from upstream. The fresh water coming down from the Taff, Ely and Rhymney may be effective in the same way and cause a gradient in oxygen saturation from the point of entry of the fresh water. The water that forms a state of low water at the station is only for a short period under the influence of these rivers, and, with the flood tide, moves up-channel outside their range. In this position it may enter a region where the effect of contaminating products causes a lower saturation.

There are, undoubtedly, gradients of other factors which have not been determined, particularly opacity, and possibly contaminating products as suggested by the higher phosphate and lower oxygen saturation at low water. While it is not possible to define all the gradients individually, the values for the height of the tide summate the effects of the gradients as a whole.

The water within the investigated length cannot be regarded as distinct and isolated. It becomes mixed with, and replaced by, partially or ultimately completely, up- or down-channel water. This process is, in the last place, dependent on the fresh water flowing into the estuary and channel on the up-channel side. When the up-channel water is dominant there is a drop in salinity in the investigated length. With decreasing rainfall the effect of the up-channel water is lessened, and the down-channel water mixes with, and replaces, the water in the investigated length, thus increasing the salinity. The measure of the dominance of one or other body of water is given by the average monthly salinities (Table I), and changes in values indicate that up-channel water entered the investigated length from September to February, and that down-channel water entered from February to the end of the period. Apparently this process had an annual cycle. The water that entered the investigated length from up- or down-channel brought in with it its own plankton, which mixed with the plankton already there, and gave to this mixed plankton a new environment. This process is referred to as the annual cyclical movement.

An outflow of less saline water along the surface of the channel, as in the Tees estuary (Alexander *et al.* 1935), appeared to play a negligible part and occurred only under exceptional conditions. This is easily understandable since the bulk of fresh water enters the channel far above the investigated length, and the mixing processes, induced by the tidal streams, would cause any such layer to lose its identity before arriving at the investigated length.

The correlations in Fig. 5 show how the diatoms can be related to one another within the investigated length. The percentages of *Biddulphia sinensis* and *B. regia* in the samples agree in being inversely correlated, and the percentages of *Rhizosolenia setigera* and *Bacillaria* agree in being directly correlated with the height of the tide. Two periods are distinguished. From February to May the correlations determine that *Biddulphia sinensis* was more up-channel than *Bacillaria*, and from June to August that *Biddulphia regia* was more up-channel than *Rhizosolenia setigera*.

Biddulphia sinensis → *Bacillaria*.
Biddulphia regia → *Rhizosolenia*.

Further, from the correlations in Fig. 6 it is clear that, in their respective periods, *Biddulphia sinensis* and *B. regia* were more frequent on the up-channel side, and *Rhizosolenia* and *Bacillaria* on the down-channel side.

Of the copepods only *Eurytemora* varies sufficiently along the investigated length to permit of analysis. Fig. 10 indicates, from the direct correlation, that the surface *Eurytemora* were more frequent down-channel than up-channel. This appears to be quite inconsistent with the known behaviour of *Eurytemora* in other areas (Percival, 1929). When, however, the total *Eurytemora* obtained, both from surface hauls and deep hauls, are plotted against the height of the tide (Fig. 11) an inverse correlation appears which shows that actually *Eurytemora* was a more up-channel form. The direct correlation between the height of the tide and the percentage of the total *Eurytemora* at the surface (Fig. 11) shows that the farther down-channel the more evenly were the *Eurytemora* distributed from the surface to the bottom. On the up-channel side of the investigated length the large majority of the *Eurytemora* was at the bottom. It is this variation in vertical distribution along the investigated length which explains the difference in correlations between the surface *Eurytemora*, the total *Eurytemora*, and the height of the tide.

From the plankton results the annual cyclical movement is illustrated best by the copepods. Since the changes in average monthly salinities measure the influx of up- or down-channel water, a comparison of Fig. 9 with the average salinities for the corresponding months (Table I) suggests that the copepod succession from up-channel to down-channel was

Eurytemora → *Acartia* → *Euterpina*.

This evidence is insufficient, since some factor, such as temperature, may determine the succession, but the composition values for July 27 (Table XI) do, however, substantiate the suggestion and allow the addition

Euterpina → *Oithona*.

Since *Centropages hamatus* followed *Oithona* in time, the succession can probably be further extended to

Oithona → *Centropages*.

It is of interest that, working at one place in the channel, a succession of copepods was obtained which illustrates part of the range from purely brackish water species to purely oceanic species (see Russell, 1936, quoting Ostenfeld, 1931).

Brackish water, e.g. *Eurytemora affinis*.
Littoral, and brackish water, e.g. *Acartia bifilosa*.
Neritic, low salinity, e.g. *Oithona nana*.
Neritic, e.g. *Centropages hamatus*.

The data which have been presented indicate the importance of space, and an ideal figure representing the changes in the plankton should be three dimensional, with a consideration of the changes in relation to both time and space. Apart from the difficulties of constructing such a figure, the available data are not sufficient for such a construction. In Fig. 12 is shown a strictly diagrammatic attempt, without attention to scale, to give the arrangements of the four main diatoms. *AB* represents the investigated length of channel concerned from February to the end of April, with *A* on the up-channel side, and *CD* represents the length between June 18 and the end of the period, with *C* on the up-channel side. The sections *AB* and *CD* depend on the relations shown in Fig. 5 and Fig. 6.

If the change in the diatoms *AB* to *CD* was continuous, then some such arrangement as in *BC* seems possible. It is to be understood that the sections *AB* and *CD* are the assumed arrangements at any point instant of time, and are, therefore, purely spatial arrangements. They are synthesized from a number of observations. The spatial arrangement in the interval between the conditions in *AB* and *CD* cannot be determined from available observations, and, since the hypothetical arrangement in *BC* represents a process of change, the time element cannot be neglected. It may be expected that *AD* represents the length of channel involved in the annual cyclical movement, thus making the arrangement in *BC* also spatial. If this was so, then it is clear *Bacillaria* should have been more up-channel than *Biddulphia regia.*

Against the height of the tide in Fig. 13 are plotted the number of *Biddulphia regia* to one *Bacillaria* on each occasion from June 3 to the end of the survey. The inverse relation indicates that the farther up-channel, the more *Biddulphia regia* were there compared with *Bacillaria.* Therefore, *Biddulphia regia,* even in this period, was more up-channel than *Bacillaria.* This means that the decrease of *Bacillaria* was not due to a movement up-channel out of the investigated length, but an actual decrease independent of, at least directly, the annual cyclical movement. In this it agreed with *Biddulphia sinensis,* which decreased from November onwards, and was, therefore, also independent of the annual cyclical movement. It should be noticed that, provided the idea of the annual cyclical movement is true, the decrease in *Bacillaria* was more extensive than the figures indicate. Since it was during the whole period a down-channel form, *Bacillaria* should have increased in numbers with the inflow of down-channel water, in agreement with the extension of the gradient in numbers along the investigated length (Fig. 5). That the decrease in *Bacillaria* cannot be considered as a change dependent on space does not deny the possibility that the annual cyclical movement was largely concerned in the change from *AB* to *CD.* The succession shown in the copepods would be expected to have its counterpart in the diatoms.

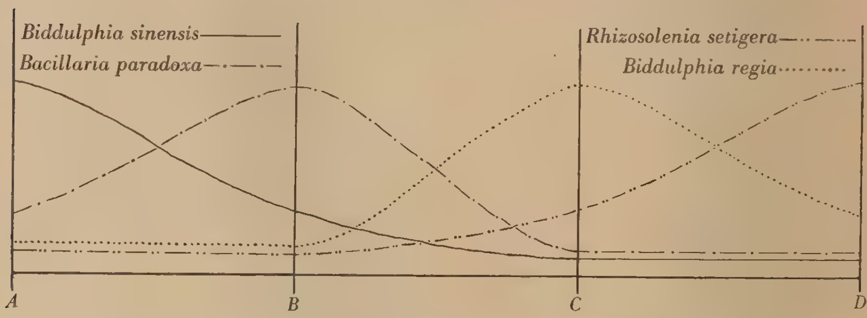


Fig. 12. Diagrammatic representation of the arrangement of the diatoms. See text.

While it is recognized that the section *BC* is hypothetical, it is considered that the sudden increase of *Rhizosolenia setigera* on April 25 (Fig. 5) does not necessarily deny the possibility of a continuous change from *AB* to *CD.* Such sudden changes in numbers of some species occurred on occasions without corresponding changes in associated forms. *Eurytemora* decreased suddenly on May 27 and *Acartia* increased on May 21 (Table X), *Podon* *polyphemoides* and ascidian larvae appeared suddenly on June 18, post-larval asteroids and ascidian larvae were found on September 26 (Table XII) and *Rhizosolenia* increased in numbers again on July 19 (Figs. 5, 6).

The consideration of the extent of phytoplankton production involves both a consideration of the actual density of the population and the variations in production throughout the year. On the first question the centrifuge counts (Fig. 8) clearly indicate a marked poverty. The maximum number of 72 chains per 20 c.c. may be compared with the frequent numbers of over 10,000 per 20 c.c. of Marshall & Orr (1927) and Steeman Nielsen (1935).

The second question is complicated by the cyclical movement, and it is necessary to neglect space and consider chiefly time. In so far as the results from samples can be accepted, it appears from Table VIII and Fig. 4 that there was no spring maximum, and that, though there was an increase in numbers from January onwards, there was no sudden rise such as usually occurs in other areas. It is, of course, clear that, because of the annual cyclical movement, the amount of production cannot be deduced from such factors as the phosphate, as was done in general terms by Hardy (1935) and in detail by Harvey (1934*b*).

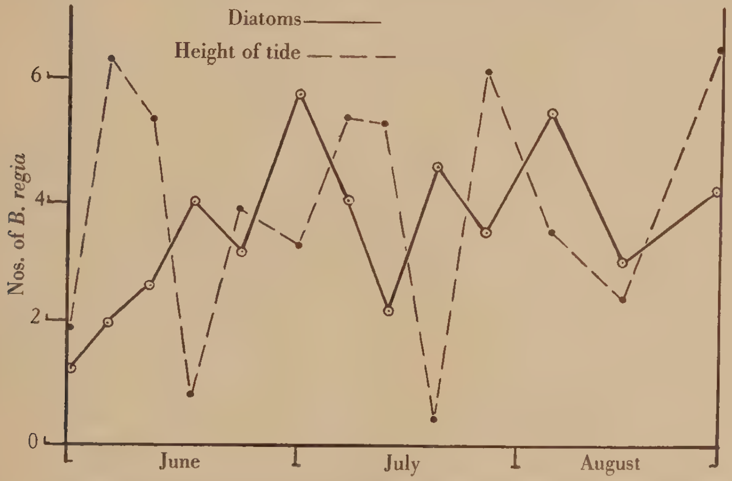


Fig. 13. The relation between the height of tide and the number of *Biddulphia regia* to one *Bacillaria paradoxa* chain in the samples from June 3 to August 25.

The major inhibiting factor on the phytoplankton production must be considered to be the instability of the water which is caused by the tidal streams. Since Gran's (1931) insistence on the importance of this factor, a considerable body of work has accumulated illustrating this. We may select as examples Steeman Nielsen (1935) and Hart (1934). The action of this factor is to remove the diatoms away from the photosynthetic zone into a deeper zone, where photosynthesis cannot take place, thus giving the diatoms less time for effective assimilation. The results of Steeman Nielsen (1935) are particularly striking. He found, for example (p. 70), that the spring increase occurred a month earlier in the stable Icelandic fjords than in the open coastal water, and production begins here only when the water is stabilized.

Owing to the shallowness of the Bristol Channel in the area concerned, instability in itself is not a sufficient explanation, since what is really effective is the ratio between the depth of the photosynthetic zone and the depth of swirling of the diatoms. Arising from the instability is the excessive quantity of silt and detritus in suspension, and it is this that makes the photosynthetic zone into a small layer and so increases the ratio. As it is the ratio which is effective, the conditions of production down-channel are not necessarily better than up-channel, in spite of the gradient of transparency, since farther down-channel the water is deeper. The gradient of decreasing phosphate must also be kept in mind.

The phytoplankton production is, therefore, largely controlled by the opacity, a factor which, in itself, has received much emphasis (Marshall & Orr, 1928; Pettersson, Höglund & Landberg, 1934), and the instability. These restrictions on production may be taken as approximately constant throughout the year. The nutritive salts, or, at least the phosphates and by implication the nitrates, were not limiting factors at any time, and, as far as the data go, light appears to be controlling within the limits imposed by the instability. An increase in the amount of light gave rise to an increase of photosynthesis, but, since the effectiveness of the light was reduced by the instability, the increase in photosynthesis did not correspond in degree with the increase of light. The absence of a limiting effect by the nutritive salts permitted the increased photosynthesis, such as it was, to proceed through the summer months and so give a form of diatom numbers shown in Fig. 4.

A contributory factor may be the salinity. Since the diatoms are typically marine, the lower the salinity the greater is the deviation of the environment from normal, but, while this may itself restrict production, the chief effect, probably, is to restrict the number of species and to debar species which might otherwise engage in a sudden increase. The suspended material may restrict certain species and this, possibly, partially accounts for the poverty in the number of species, particularly in the zooplankton. Ostenfeld (1931) maintains that the absence of several organisms in the eastern part of the English Channel and southernmost North Sea is due to this cause.

It would appear that the causes of the poverty of the fauna and flora in the plankton is due to the instability, with resulting siltiness, and the low salinity. The bacteriological examination of the water indicates sewage pollution, but, since the oxygen saturation is not appreciably lowered, it is unlikely that this pollution acts as an inhibitory factor. Sewage pollution may, in fact, favour plankton production. Välikangas (1926) has found that in the harbour of Helsingfors the greatest production of plankton takes place in the Bay of

Tölö where the greatest amount of sewage from the town of Helsingfors is poured out.

A note on the quantitative method may not be out of place. The poverty of the phytoplankton and the amount of suspended matter present considerable difficulties. Analyses of small samples of water, as in the centrifuge and sedimentation processes, would not give results of the type such as have been here presented, especially as the volume, small as the processes demand, is made smaller by the amount of silt that would be deposited. The silt introduces difficulties, also, in filtration of larger samples of water, since, even with a filter of 100 meshes to the inch, the volume of inanimate matter was usually greater, and often several times greater, than the volume of plankton, with resulting difficulties in the analysis of the samples. The use of a fine filter or phosphorbronze (Hentschel, 1936) would therefore defeat its own object, and towing with a very fine net would have a similar result. Possibly the only improvements on the method, as far as present methods go, would be the use of a meter (Harvey, 1934*a*) or a centrifugal pump (Gibbons & Fraser, 1937).

It is recognized that the method resulted in a selection of the diatoms, missing out comparative samples of, for example, *Skeletonema costatum*, and collecting the larger diatoms. However, the majority of the diatoms listed in Table XII would have been caught at least as efficiently as *Bacillaria* and *Rhizosolenia setigera*, and an accumulation of these would have given an indication of a sudden rise in numbers had there been one. Gran (1932, p. 346) maintains that "The total sum of all species could not be used to measure the productivity of an area of the sea any better than the study of the growth and decrease of the dominant species". The present discussion on phytoplankton production depends upon this.

ACKNOWLEDGEMENTS

I take the greatest pleasure in acknowledging my indebtedness to Prof. W. M. Tattersall who has given me the considerable advantages of his personal instruction, help and encouragement in the course of this work and previously. I am also deeply obliged to my present colleagues, Mr C. E. Lucas and Mr N. B. Marshall, for affording me ample opportunity for discussing with them, to my great advantage, the various problems arising from the results.

The field and laboratory work was done while I held a Post-graduate Studentship of the University of Wales.

SUMMARY

The plankton collected at a station in the Bristol Channel in 1936–7 is related to chemical and hydrographical factors.

On account of the varying speeds of the tidal streams, the observations

refer, not to a single point, but to a series of points along a length of the channel.

Gradients of salinity, phosphate, and a possible complicated gradient of oxygen saturation, were determined, and, from the average monthly salinities, an annual cyclical movement of water deduced.

From February to June *Biddulphia sinensis* was a more up-channel form than *Bacillaria paradoxa*, and, from June to August *Biddulphia regia* was more up-channel than *Rhizosolenia setigera*. In this latter period *Biddulphia regia* was more up-channel than *Bacillaria*.

From being concentrated at the bottom on the up-channel side *Eurytemora* became more and more evenly distributed from the surface to the bottom on the down-channel side.

Owing to the annual cyclical movement, a succession of copepod species from up-channel to down-channel entered the investigated length.

The decrease in numbers of *Biddulphia sinensis* and *Bacillaria* was, directly, independent of the annual cyclical movement, but this movement may have been effective to some extent in transforming the diatom population.

The instability of the water and the opacity, which result from the tidal streams, are the major inhibiting factors on diatom production. Low salinity and excessive siltiness are possible contributory factors.

Phosphate was not, at any time, a limiting factor, and diatom production was, apparently, controlled by light within the limits imposed by the inhibiting factors.

The bacteria indicate some sewage pollution.

REFERENCES

Alexander, W. B., Southgate, B. A. & Bassindale, R., 1935. Survey of the river Tees. Part II. The estuary-chemical and biological. *Water Pollution Research Tech. Paper*, No. 5, i–xiv, pp. 1–171.

Alsterburg, G., 1926. Die Winklersche Bestimmungsmethode für im Wasser gelösten Sauerstoff, usw. *Biochemische Zeitschrift*, Vol. clxx, pp. 30–75.

Atkins, W. R. G., 1923. The phosphate content of fresh and salt waters in its relationship to the growth of algal plankton. *Journ. Mar. Biol. Assoc.*, Vol. xiii, pp. 119–50.

Dianova, E. & Voroshilova, A., 1935. Salt composition of medium and specificity of marine bacteria. *Mikrobiol.* (*U.S.S.R.*), Vol. iv, p. 393.

Fox, C. J. J., 1907. The dissolved gases of sea-water. *Public. de Circons.*, No. 41, pp. 1–23.

Gibbons, S. G. & Fraser, J. H., 1937. The centrifugal pump and suction hose as a method of collecting plankton samples. *Journ. Cons. Int. Explor. Mer.*, Vol. xii, No. 2, pp. 155–70.

Gran, H. H., 1931. On the conditions for the production of plankton in the sea. *Rapp. Proc.-Verb. Int. Cons. Explor. Mer.*, Vol. lxxv, pp. 37–46.

—— 1932. Phytoplankton. Methods and problems. *Journ. Cons. Int. Explor. Mer.*, Vol. vii, No. 3, pp. 343–58.

Gurney, R., 1931. *British Freshwater Copepods*, Vol. i, Ray Soc., pp. 1–238.

HARDY, A. C. & GUNTHER, E. R., 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927. *Discovery Reports*, Vol. XI, pp. 1–456.

HART, T. J., 1934. On the phytoplankton of the south-west Atlantic and the Bellinghausen Sea, 1929–1931. *Discovery Reports*, Vol. VIII, pp. 1–268.

HARVEY, H. W., 1934*a*. Measurement of phytoplankton population. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 761–73.

—— 1934*b*. Annual variation of planktonic vegetation, 1933. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 775–92.

HENTSCHEL, E., 1936. Zur quantitativen Planktonmethodik. *Kieler Meeresforsch.*, Bd. I, pp. 322–6.

JORGENSEN, O. M., 1929. Plankton of the river Tyne estuary. *Proc. Univ. Durham Phil. Soc.*, Vol. VIII, pt. 1.

LLOYD, B., 1930. Bacteria of the Clyde Sea area. A quantitative investigation. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 879–907.

MARSHALL, S. M. & ORR, A. P., 1927. The relation of the plankton to some chemical and physical factors in the Clyde Sea area. *Journ. Mar. Biol. Assoc.*, Vol. XIV, pp. 837–68.

—— —— 1928. The photosynthesis of diatom cultures in the sea. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 321–60.

MCCLENDON, J. F., 1917. The standardization of a new colorimetric method for the determination of hydrogen-ion concentration, etc., of sea water. *Journ. Biol. Chem.*, Vol. 30, pp. 265–88.

MEEK, A., 1923*a*. Estuarine plankton. *Dove Mar. Lab. Report for* 1923, pp. 78–91.

MEEK, E. M., 1923*b*. Pollution in the river Tyne. *Dove Mar. Lab. Report for* 1923, pp. 53–66.

MINISTRY OF HEALTH, 1936. The bacteriological examination of water supplies. *Reports on Public Health and Medical Subjects*, No. 71.

NIELSEN, E. STEEMAN, 1935. The production of phytoplankton at the Faroe Isles, Iceland, East Greenland and the waters around. *Medd. Komm. Danmarks Fisk.- og Havunders, Ser. Plankton*, Vol. III, Nr. 1, pp. 1–93.

OSTENFELD, C. H., 1931. Résumés des observations sur le plankton des Mers explorées par le Conseil pendant les années 1902–8. *Cons. Perm. Int. Expl. Mer. Bull. Trim.*, Pt. 4.

PERCIVAL, E., 1929. A report on the fauna of the estuaries of the river Tamar and the river Lynher. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 81–108.

PETTERSSON, H., HÖGLUND, H. & LANDBERG, S., 1934. Submarine daylight and the photosynthesis of phytoplankton. *Göteborg Vetensk. Samh. Handl.*, 5. B, Bd. 4 (5), pp. 1–17.

RUSSELL, F. S., 1936. A review of some aspects of zooplankton research. *Rapp. Proc.-Verb. Cons. Int. Explor. Mer.*, Vol. XCV, pp. 3–30.

VÄLIKANGAS, I., 1926. Planktologische Untersuchungen im Hafengebiet von Helsingfors. I. Ueber das Plankton insbesondere das Netz-Zooplankton des Sommerhalbjahres. Helsingforsiae 1926. *Acta Zoologica Fennica*, 1, pp. 1–298.

WELLS, A. L., 1938. Some notes on the plankton of the Thames estuary. *Journ. Animal Ecol.*, Vol. VII, pp. 105–24.

WILSON, D. P., 1929. The larvae of the British Sabellarians. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 221–51.

ON THE GROWTH AND FEEDING OF YOUNG HERRING IN THE CLYDE

By S. M. Marshall, D.Sc., A. G. Nicholls, Ph.D. and
A. P. Orr, M.A., D.Sc., A.I.C.
Marine Station, Millport

(Text-figs. 1–12)

CONTENTS

	PAGE
Collection of material	427
Race determination	429
Size and growth	434
Weight	438
Chemical composition	442
Food and its relation to the plankton	445
Summary	453
References	453

In an earlier paper (Marshall, Nicholls & Orr, 1937) the growth of the herring in the Clyde was followed from spawning to metamorphosis. The present paper gives the results of an attempt to continue this work from metamorphosis up to the formation of the first winter ring.

During the course of the work two distinct groups of herring were met with. Those of the first, which were obtained from July 1936 to May 1937, were caught in Kames Bay and on Fairlie Sands; the second, of which only a few catches were taken, in 1937 and 1938, were smaller and were caught offshore. As will be shown below, the second group is composed of herring which were spawned in the Clyde sea-area in spring and are therefore of the same origin as those discussed in the previous paper.

Collection of Material

Larvae which had been followed from hatching off Brown Head on the coast of Arran to metamorphosis in the mouth of Loch Fyne about the beginning of June 1935 disappeared thereafter. In spite of an intensive search of the area during the following months, both in sandy bays using a fine-meshed shore seine and in deeper water using a Poole sprat trawl, very few were found. In July 1936, however, young herring about 80 mm. long were captured in Kames Bay, a shallow sandy bay on the island of Cumbrae. From then on successful hauls were made at about weekly intervals in the same bay till the end of September when numbers became very small. Thereafter till the following May they could be caught near Hunterston Perch on Fairlie Sands on the Ayrshire coast. At this position the sand-flat shelves steeply down to a depth of several fathoms, and hauls were always made at low tide when it was possible to use the shore seine on the slope. The best hauls were taken about dusk or dawn on moonless or overcast nights. On several occasions both in Kames Bay and on Fairlie Sands the herring disappeared as soon as the moon rose.

Catches on Fairlie Sands were not obtained so regularly as in Kames Bay and it was sometimes necessary to make hauls on several nights before a catch was obtained. Sometimes an indication of herring was given by gannets diving, by the presence of seals or by hearing the fish break the surface. The catches were smaller after November 1936, and after May 1937 they were irregular. By the end of May the new brood of young herring appeared again in Kames Bay and these were followed for a few weeks to compare with the previous year's fish.

The number of herring in a haul with the fine-meshed shore seine varied very considerably. Sometimes several hauls were required to obtain sufficient fish for a sample (a few hundred), but occasionally many thousands were captured in a single haul.

Other types of gear were tried with varying degrees of success. A Saltash tuck seine with a fine-meshed bag proved unsuccessful in spite of being used immediately after the shore seine had made a successful haul. A Poole sprat trawl was uniformly unsuccessful even at times when herring were present in large numbers. A series of drift nets with mesh varying from 57 to 75 rows per yard was useful offshore, but since the shore seine provided an unselected sample the use of drift nets was discontinued.

For offshore work a sprat ring net similar to that used at Newhaven, in the Firth of Forth, was used and was successful at times when the herring could be located by means of phosphorescence in the water. Unfortunately the mesh in the bag of the net was too large (90 rows per yard) to retain all the smallest fish so that sampling for these was not accurate. Successful catches of the small offshore fish were made in July and August 1937 in Loch Striven, the Kyles of Bute and round the Cumbrae, and in October 1937 and March 1938 in Loch Striven.

To find the fluctuations of numbers with time of night and to provide material for a study of the food over a night, a series of hauls was made at 2 hr. intervals in Kames Bay on August 14 1936 (Fig. 12 A). At 5 p.m. (B.S.T.), although it was full daylight and there were a number of bathers and small boats in the bay, 132 herring were caught in one haul; at 7 p.m. the number rose to 4000–5000. The best catch (estimated at over 10,000 fish) was obtained at 9 p.m., the time of sunset. After this catches decreased rapidly; at 11 p.m. when it was quite dark, there were 450; at 1 a.m., 8; at 3 a.m., 12. At 5 a.m. when dawn was breaking there was a slight increase to 293, but by 7 a.m. there was a decrease again to 6 and hauls were discontinued.

RACE DETERMINATION

As has already been mentioned, the young herring captured in the Clyde belong to two different groups which may conveniently be described as inshore and offshore. The inshore fish were considerably larger than the offshore fish and it became necessary to find out whether two distinct races of herring were present, and if so which, if either, represented the Clyde spring-spawned fish.

In defining different races of herring, one of the most usual methods is to count the number of vertebrae in a representative sample of fish; the mean number is indicative of the race. Wood (1936) found the mean number of vertebrae in spring-spawning herring in the Clyde to vary between 57·03 and 57·21. It should be noted that Wood follows Williamson (1914) and Johansen (1919) in including the first segment of the terminal ossicle in the vertebral count. In this paper we have followed Orton (1916) and Ford (1928*a*) in excluding it. Four samples of adult Clyde herring taken in the autumn of 1937 and the spring of 1938 gave counts from 55·88 to 56·06, which shows a good agreement with Wood's figures when the necessary allowance of one vertebra is made. A statistical comparison (see Ford, 1928*a*, p. 259) showed that these four samples agreed well with one another and with Wood's samples.

Counts were also made on samples of the young herring caught and it was found that the herring of the offshore group had a vertebral count varying from 55·97 to 56·16 showing agreement with the Clyde spring-spawned fish. Those caught in Kames Bay and on Fairlie Sands (the inshore group) belonged to a different race with a lower vertebral count varying from 55·40 to 55·65.

In Fig. 1 are shown percentage frequency graphs of the number of vertebrae based on the commercial catches of Clyde fish (A), the offshore samples of young herring (B), and the inshore samples (C). The results of the individual counts are given in Table I. It will be seen that whereas curves (A) and (B) show a sharp peak, as is typical of Wood's spring spawners, (C) is of a quite distinct type. There seems little doubt therefore that the offshore fish are Clyde spring-spawned herring. Similar counts to those of the offshore fish were obtained on the 1935 brood in three successive years (Table I, C). As premetamorphosis fish they were caught in Loch Fyne in 1935 (May 30), as one year old fish in Kames Bay in 1936 (August 10), and as two year old fish in Millport Bay in 1937 (May 26), and the vertebral counts were 56·07, 56·07 and 55·97 respectively.

The curve shown by the inshore fish (C) is similar to Wood's autumn-spawning type. There is, however, little evidence of any autumn spawning in the Clyde. Tow-nettings were taken for larvae and the gonads of adult fish examined in autumn, but no indication was obtained that any spawning takes place before March. Wood (1937, p. 18) believes that the Clyde "estuary" is a nursery for adolescent herring groups until they reach sexual maturity.

It is possible therefore that the origin of these herring is to be sought outside the Clyde. Samples of adult herring were obtained from the North of Ireland fisheries in April and September 1938, and from the Isle of Man fisheries in April and July 1938. The first were spent and their vertebral count showed the typical curve for spring-spawning herring (average number of vertebrae 55·97). The second were mostly full and showed the autumn-spawning type of curve (average number of vertebrae 55·63). The Isle of Man fish were spent in April and recovering spents at the beginning of July and showed the typical autumn-spawning type of curve (average number of vertebrae 55·49 and 55·53 in April and July respectively). A statistical comparison showed that the North of Ireland fish in September and both lots of Isle of Man fish agreed

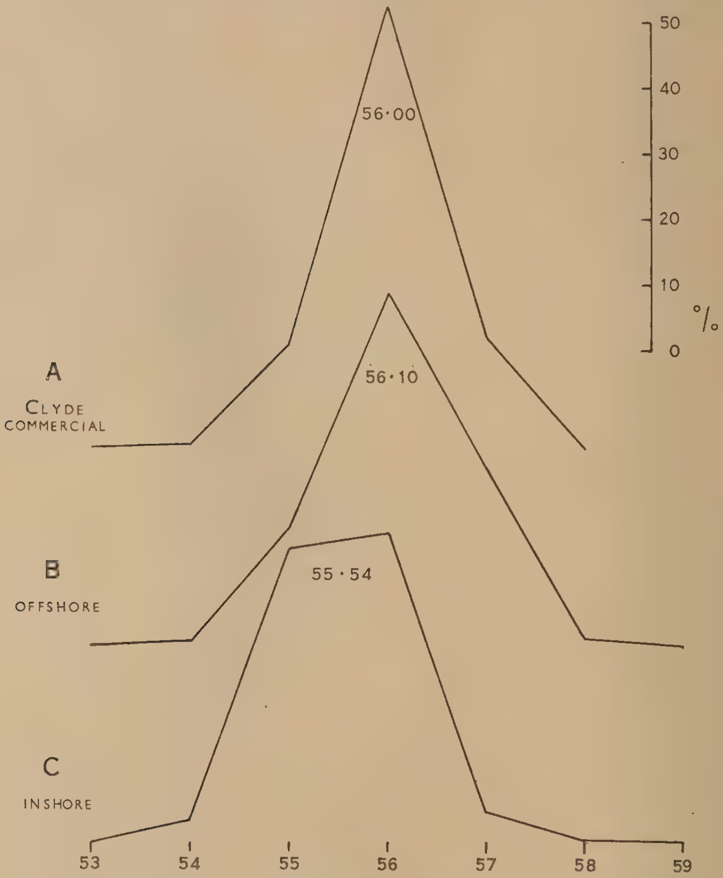


Fig. 1. Percentage frequency distribution curves of vertebral counts.

TABLE I

A. VERTEBRAL COUNTS OF INSHORE HERRING

Date	No. of fish	Percentage number of vertebrae									Mean	σ
		52	53	54	55	56	57	58	59	60		
13–14 & 14. vii. 36	102	..	..	2·0	47·1	44·1	6·9	..	..	..	55·56	0·654
20. vii. 36	106	..	..	0·9	41·5	52·8	4·7	..	..	..	55·61	0·595
27. vii. 36	103	..	..	7·8	44·7	42·7	2·9	1·0	..	1·0	55·49	0·850
10. viii. 36	111	..	..	2·7	51·4	41·5	4·5	..	..	..	55·48	0·630
14. viii. 36	109	..	..	4·6	37·6	52·3	5·5	..	..	..	55·59	0·670
31. viii. 36	110	..	..	6·4	40·9	49·1	3·6	..	..	..	55·50	0·674
23. ix. 36	111	..	..	4·5	48·7	42·4	4·5	..	..	..	55·47	0·658
29. ix. 36	111	..	..	4·5	37·8	52·3	5·4	..	..	..	55·59	0·667
5. x. 36	110	..	..	3·6	46·4	43·6	5·5	0·9	..	..	55·54	0·700
13. x. 36	110	..	..	1·8	37·3	55·5	4·6	0·9	..	..	55·65	0·642
28. x. 36	110	..	..	1·8	49·1	42·7	6·4	..	..	..	55·54	0·645
3. xi. 36	110	..	..	0·9	40·9	51·8	6·4	..	..	..	55·64	0·617
13. xi. 36	110	..	..	2·7	56·4	39·1	1·8	..	..	..	55·40	0·578
27. xi. 36	109	..	..	1·8	43·1	51·4	3·7	..	..	..	55·57	0·599
11. xii. 36	110	..	..	4·6	42·7	49·1	2·7	0·9	..	..	55·53	0·673
28. xii. 36	110	..	..	5·5	50·9	40·9	2·7	..	..	..	55·41	0·640
12 & 13. i. 37	110	..	..	3·6	39·1	51·8	5·5	..	..	..	55·59	0·654
9. ii. 37	110	..	..	5·5	41·8	47·3	5·5	..	..	..	55·53	0·687
15. iii. 37	110	..	..	5·5	41·8	45·5	6·4	0·9	..	..	55·55	0·737
29. iii. 37	110	..	..	4·6	35·5	55·5	4·6	..	..	..	55·60	0·653
13. iv. 37	79	..	..	1·3	51·9	40·5	6·3	..	..	..	55·52	0·638
28–29. iv. 37	110	..	..	0·9	48·2	47·3	3·6	..	..	..	55·54	0·585
13. v. 37	110	..	..	3·6	43·6	45·5	6·4	0·9	..	..	55·57	0·710
27. v. 37	109	..	..	..	46·8	49·5	3·7	..	..	..	55·57	0·567
21, 22 & 25. vi. 37	110	0·9	..	0·9	40·0	55·5	2·7	..	..	..	55·57	0·656
15. vii. 37	110	..	..	4·6	51·8	40·9	1·8	0·9	..	..	55·43	0·656
28. vii. 37	83	..	..	2·4	49·4	42·2	6·0	..	..	..	55·52	0·651

From 23. ix. 36 to 13. iv. 37 inclusive and on 13. v. 37 the herring were taken from Fairlie Sands, and on the remaining dates from Kames Bay.

B. VERTEBRAL COUNTS OF OFFSHORE HERRING

Date	Source	No. of fish	Percentage number of vertebrae						Mean	σ
			53	54	55	56	57	58		
8–9. vii. 37	Loch Striven	110	..	..	20·0	46·4	30·9	2·7	56·16	0·773
2. viii. 37	The Tan	110	..	1·8	16·4	50·0	30·9	0·9	56·13	0·756
5. x. 37	Loch Striven	102	..	1·0	18·6	60·7	19·6	..	55·99	0·652
21. iii. 38	Loch Striven	251	..	..	16·7	56·6	26·3	0·4	56·10	0·661

C. VERTEBRAL COUNTS OF 1935 BROOD FISH

30. v. 35	Otter Spit	113	..	..	13·3	66·4	20·4	..	56·07	0·578
10. viii. 36	Kames Bay	106	..	..	19·8	55·7	22·7	1·9	56·07	0·707
26. v. 37	Millport Bay	110	..	..	15·5	71·8	12·7	..	55·97	0·533

D. VERTEBRAL COUNTS OF COMMERCIAL SAMPLES

15. x. 37	Clyde	100	..	..	12·0	73·0	15·0	..	56·03	0·521
9. xi. 37	Clyde	108	..	..	26·9	58·4	14·8	..	55·88	0·637
10. iii. 38	Clyde (Brown Head)	110	..	0·9	11·8	70·9	16·4	..	56·03	0·566
16. iii. 38	Clyde (Ballantrae Banks)	110	..	0·9	12·7	65·5	20·9	..	56·06	0·610
8. iv. 38	Isle of Man	217	0·5	5·1	45·6	43·3	5·1	0·5	55·49	0·715
13 & 19. iv. 38	North of Ireland	183	..	..	20·8	62·8	15·3	1·1	55·97	0·637

with the inshore young herring from the Clyde; in addition they agree fairly well with summer-spawned Isle of Man herring examined by el Saby (1932).

Because of their proximity to one another, it might be expected that the two groups of young herring would be mixed in the catches. The distinction between the two groups of fish, however, is sharp and it seems improbable that any appreciable intermixture takes place. In July when both types of fish were caught about the same time, there was hardly any overlapping in the size frequency distribution curve (see Table II and Fig. 2). The vertebral counts also are distinct in the groups and, within each group, show statistical agreement. Either then the two groups of fish keep apart or the degree of intermixture is comparatively constant. This last possibility is ruled out for the following reason. Since the offshore herring, which had a high vertebral count, are considerably smaller than the inshore fish, it would be expected that if mixing were taking place, the smaller fish of any sample would have a higher average number of vertebrae than the sample as a whole. No such difference actually exists so that we may conclude that the two groups keep apart and that mixture is negligible.

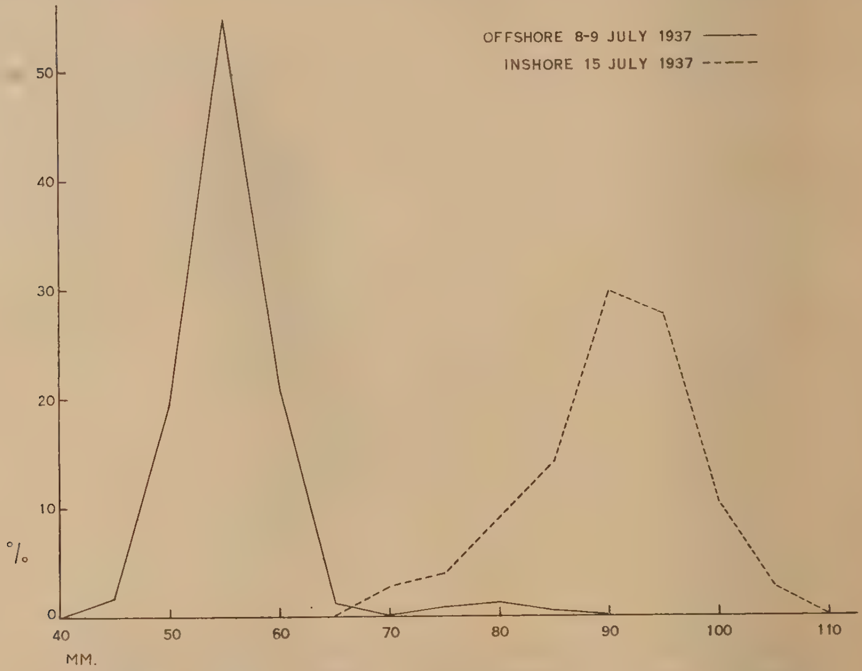


Fig. 2. Percentage frequency distribution curves of lengths for comparison of inshore and offshore young herring.

TABLE II. LENGTH MEASUREMENTS OF INSHORE HERRING

	1936										
mm.	13 & 14. vii.	20. vii.	27. vii.	3 & 4. viii.	10. viii.	14 & 15. viii.	19. viii.	24. viii.	31. viii.	8. ix.	15. ix.
55	..	1	2	..	..	..	..	..	..	..	..
60	2	1	1	1	..	..	..	..	..	..	..
65	10	1	..	1	..	..	..	..	..	..	..
70	17	13	2	2	..	..	2	..	..	..	..
75	30	56	6	12	3	9	2	..	..	..	..
80	90	86	21	47	8	20	9	..	..	..	4
85	124	155	94	109	15	32	4	1	1	..	18
90	26	226	294	175	28	79	7	4	..	..	38
95	1	92	155	134	62	128	1	9	..	4	44
100	..	7	44	33	130	238	3	38	2	14	73
105	..	..	3	6	181	397	5	80	14	29	97
110	..	..	..	..	67	245	3	110	24	71	122
115	..	..	..	..	7	60	..	78	53	77	75
120	..	..	..	..	..	1	1	39	85	81	23
125	..	..	..	..	..	..	..	2	83	47	5
130	..	..	..	..	..	..	..	1	16	17	3
135	..	..	..	..	..	..	..	..	..	1	1
140	..	..	..	..	..	..	..	..	..	..	..
145	..	..	..	..	..	..	..	..	..	..	..
150	..	..	..	..	..	..	..	..	..	..	..
155	..	..	..	..	..	..	..	..	..	..	..
160	..	..	..	..	..	..	..	..	..	..	..
165	..	..	..	..	..	..	..	..	..	..	..
170	..	..	..	..	..	..	..	..	..	..	..
Total	300	638	622	520	501	1209	37	362	278	341	503
Median	85·1	90·2	93·2	92·4	105·1	107·1	91·0	112·4	122·7	118·8	109·2
Average	83·4	88·4	92·5	91·7	103·4	105·4	92·6	111·6	121·1	117·8	107·2

	1936										
mm.	23. ix.	29. ix.	5. x.	13. x.	28. x.	3. xi.	11. xi.	13. xi.	27. xi.	11. xii.	28. xii.
55	..	..	..	..	..	..	..	..	..	..	..
60	..	..	..	..	..	..	..	..	..	..	..
65	..	..	..	..	..	..	..	..	..	..	..
70	..	..	..	..	..	..	..	..	..	..	..
75	..	..	..	..	..	..	..	..	..	..	..
80	..	..	..	..	..	..	..	..	..	..	..
85	..	..	..	..	..	..	..	..	..	..	..
90	..	..	..	..	..	..	..	..	..	..	..
95	..	..	..	..	..	..	1	..	1	..	..
100	2	..	..	..	..	..	..	..	..	..	1
105	1	1	1	..	..	..	1	..	1	..	1
110	8	6	..	1	..	1	3	..	4	..	3
115	29	38	4	7	1	2	17	2	12	3	26
120	74	64	13	45	4	11	58	13	46	16	49
125	94	98	80	142	46	55	90	56	108	65	109
130	32	65	129	218	94	62	40	91	127	120	81
135	10	16	58	169	88	70	18	65	74	53	40
140	..	..	11	19	46	35	6	38	21	36	8
145	..	..	..	1	7	13	1	20	11	21	1
150	..	..	..	..	..	2	..	..	2	5	..
155	..	..	..	..	..	..	1	..	..	2	..
160	..	..	..	..	..	..	..	..	..	..	..
165	..	..	..	..	..	..	..	..	..	..	..
170	..	..	..	..	..	..	..	..	..	..	..
Total	250	288	296	602	286	251	236	285	407	321	319
Median	125·8	126·8	131·8	132·8	134·9	134·5	127·1	133·7	131·1	133·3	128·4
Average	124·8	125·8	131·2	131·7	134·6	133·9	126·8	133·9	130·8	133·9	128·1

	1937											
mm.	12 & 13. i.	9. ii.	15. iii.	29. iii.	13. iv.	29. iv.	13. v.	26 & 27. v.	31. v.	21, 22 & 25. vi.	15. vii.	28 vii.
55	..	..	..	..	..	..	..	..	..	3	..	..
60	..	..	..	..	..	..	..	..	..	16	..	..
65	..	..	..	..	..	..	..	..	..	26	..	..
70	..	..	..	..	..	..	..	..	..	89	4	..
75	..	..	..	..	..	..	..	..	..	84	6	..
80	..	..	..	..	..	..	..	..	..	31	14	2
85	..	..	..	..	..	..	..	..	..	4	22	1
90	..	..	..	..	..	..	..	..	..	..	46	12
95	..	..	..	..	..	..	..	..	..	..	43	17
100	..	..	..	..	..	..	..	..	..	..	16	25
105	..	..	1	..	..	..	..	..	..	..	4	18
110	1	1	2	..	..	1	2	..	..	..	..	4
115	..	4	4	..	2	7	8	..	..	..	..	2
120	8	13	24	4	6	15	27	1	1	..	..	..
125	23	65	46	56	20	27	59	3	9	..	..	..
130	55	67	63	121	28	26	75	6	9	..	..	..
135	41	45	39	90	25	34	48	12	27	..	..	..
140	22	19	16	32	9	32	64	10	36	..	..	..
145	21	4	4	6	2	12	27	27	40	..	..	..
150	4	..	2	3	..	2	9	42	20	..	..	..
155	1	..	..	..	..	..	2	102	8	..	..	..
160	..	1	..	..	..	1	1	55	3	..	..	..
165	..	..	..	..	..	..	1	20	3	..	..	..
170	..	..	..	..	..	..	..	3	..	..	..	..
Total	176	219	201	312	92	157	323	281	156	253	155	81
Median	135·2	132·0	132·0	134·0	133·3	135·6	134·4	156·9	144·5	74·6	94·1	101·3
Average	135·7	131·8	131·2	133·8	132·6	134·3	134·8	154·7	143·7	73·8	92·1	100·5

On two occasions (August 10 1936 and May 26 and 27 1937) offshore and inshore herring were obtained in numbers in the same hauls. On each occasion, however, they belonged to different year groups, as was discovered by scale examination, and the older fish were always offshore fish. These are smaller than inshore fish of the same age and in both sets of hauls were of similar size to inshore fish of the preceding year class. This mixture then was probably due to the tendency of herring of similar size to shoal together irrespective of age (Ford, 1928*b*, p. 291). In the catches from Kames Bay and Fairlie Sands it was usual to find a few fish belonging to the previous year class. These were omitted from the samples and they were never numerous enough for reliable size measurements or vertebral counts.

A considerable number of the backbones examined (25% in the inshore fish and 19% in the offshore fish) showed complex vertebrae, i.e. vertebrae which, although the centrum shows no sign of division, have double spines dorsally, ventrally or both (Ford, 1933). These complex segments are not uncommon among herring and if they are counted as one vertebra the vertebral counts are too low. It has been found (Kändler, 1932; Ford, 1937) that if they are counted as one and a half vertebrae the normal average is obtained, and our results confirm this. The difference between the average of those with normal and those with abnormal vertebrae (when the latter are counted as one) was in inshore fish 0·49 and in offshore fish 0·46. In Table I, however, the complex vertebrae are given the value of one. Fused vertebrae, which were very rare, are given their full value.

SIZE AND GROWTH

From each catch a sample of fish, at least 250 if possible, was taken and the length measured from the tip of the snout to the tip of the longest caudal fin ray on the ventral fluke. The fish were measured within an hour or two of capture on nearly all occasions, since it was found that standing overnight or fixation in formalin caused a shrinkage amounting to several millimetres.

Inshore herring. The results of the measurements of these fish are given in Table II and Figs. 3 and 4. In Fig. 3 are shown the median lengths of the samples of inshore and offshore herring. The upper curve which is that for the inshore herring shows that there was an increase in length from the first observation in 1936 (July) till the middle of October 1936 amounting to just over 50 mm. giving an average weekly increase of about 3·5 mm. This is slightly greater than the weekly size increment in premetamorphosis Clyde spring-spawned herring. From the beginning of November 1936 until the beginning of April 1937 there was no increase in the median length, but fish caught at the end of May 1937 were considerably larger. The catches made during April were small and it is doubtful when the new year's growth actually started. On April 13 a few of the herring and on May 14 the majority showed the new winter ring at the edge of the scale. In June and July 1937 several samples of the new brood of inshore herring were obtained and their median lengths are also shown on the curve.

In Fig. 4 are shown the size frequency distribution curves of the samples grouped in fortnightly periods, omitting for simplicity the majority of the winter samples when there was no growth. The curves show the gradual increase in length up to October and the new growth in spring. The new brood of 1937 which was caught earlier than in 1936 is also shown. The smallest fish caught, nine in number, were taken on May 27 1937 and varied from 47 to 56 mm. in length. The curves show that in general the samples were homogeneous and that the size range within a sample did not increase much during the year.

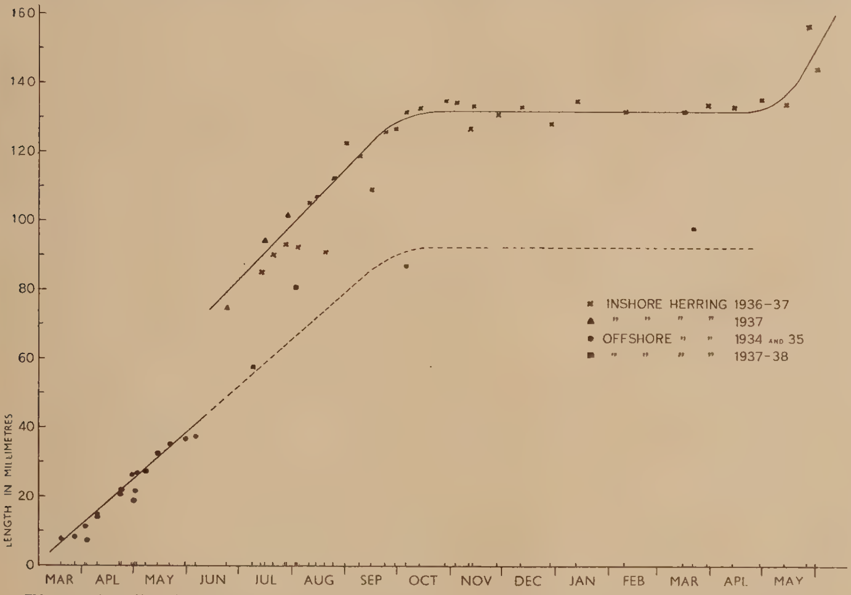


Fig. 3. Median lengths of inshore and offshore young herring, showing rate of growth.

Offshore fish. Only four catches of offshore fish in their first year were obtained, two during the growth period, one near the end of the growth period, and one near the end of the winter non-growing period. The points representing median lengths fit on an extension of the growth curve for premetamorphosis Clyde herring taken in 1935 and run parallel to but well below that for the inshore fish (Table III and Fig. 3). Thus in July 1937 the inshore fish had a median length of 94·1 mm. and the offshore fish 57·6 mm., while in March 1938, when they were forming their first winter ring, the inshore fish had a median length of about 132 mm. and the offshore about 98 mm. The size given for the offshore fish is probably on the large side since,

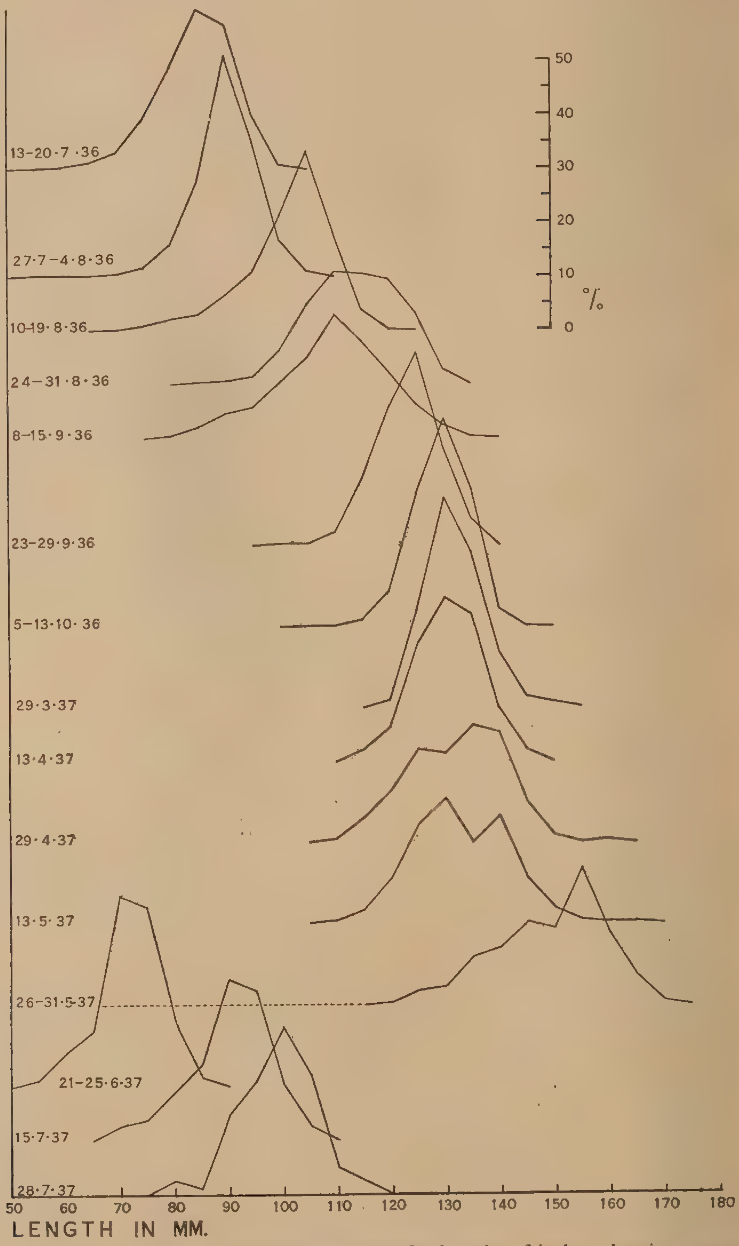


Fig. 4. Percentage frequency distribution curves for lengths of inshore herring, grouped in fortnightly periods.

as mentioned above, a proportion escaped through the meshes of the net. The 1935 brood of Clyde fish appeared again in the catches of 1936 (August 10) and 1937 (May 26 and 27); their median lengths on these dates were 131·3 and 164·4 mm. respectively.

Since the inshore and offshore herring differ considerably in length at the time the first winter ring is formed, it is possible to differentiate between the two groups at any later stage. If we assume that the rate of growth of the scale is proportional to the rate of growth of the fish (Lea, 1910), we can, by measurements on the scale, calculate the size of the fish at the end of each year's growth.

TABLE III. LENGTH MEASUREMENTS OF OFFSHORE HERRING

mm.	8, 9. vii. 37	2. viii. 37	5. x. 37	21. iii. 38
45	4	..	..	..
50	48	..	..	..
55	136	..	1	..
60	51	..	..	..
65	3	..	2	..
70	..	5	1	..
75	2	135	14	2
80	3	167	82	14
85	1	32	93	43
90	..	2	56	41
95	..	..	18	39
100	..	..	9	42
105	..	..	7	36
110	..	..	10	19
115	..	..	6	10
120	..	..	..	4
125	..	..	1	..
Total	248	341	300	250
Median	57·6	80·7	87·0	98·2
Average	57·6	80·4	88·9	98·1

Scales were taken from each fish of the measured samples of Clyde, North of Ireland and Isle of Man adult herring and the size when the first winter ring was laid down measured, using the technique described by Ford (1928*a*). The average size of the herring in the four commercial catches from the Clyde fishery at the time of formation of the first winter ring (l_1) was found to vary between 91 mm. and 110 mm. This compares with the average winter length of 93 mm. estimated for offshore herring (Fig. 3). The commercial samples from the North of Ireland fisheries gave average l_1 values of 121 mm. and 122 mm. Those from the Isle of Man fishery gave average l_1 values of 122 mm. and 120 mm., figures above those obtained from the Clyde commercial catches and the Clyde offshore fish, and nearer that for the Clyde inshore young herring (132 mm., Fig. 3). The results are not conclusive but further confirm the Clyde origin of the offshore fish and lend some support to the possibility that the inshore herring may have originated in the Isle of Man or North o Ireland grounds as was suggested by the vertebral counts.

Information on the rate of growth of herring during their first year is rather meagre. Among the earliest records are those of Meyer (1878) on spring-spawned herring in the Baltic. The rate of growth found by him for the period June 11 to November 14 (2·5 mm. per week) is lower than that found for Clyde spring-spawned herring (offshore type). On the other hand, at the end of the first year the Baltic herring reached a length of 138 mm., whereas the Clyde spring-spawned herring measured only 98 mm. The discrepancy is due to the Baltic herring growing during the winter, whereas those in the Clyde do not. Ford (1928*c*) measured the rate of growth of young herring from the Tamar and Lynher estuaries during their first year. The spawning at Plymouth in 1926–27 extended from October to March, so that the difference in age between the youngest and oldest might be several months. The median length of the Tamar fish on May 26 was 55·9 mm. and on October 7 127·1 mm., giving an average weekly increment during the growth period of 3·2 mm. which is close to that for the inshore Clyde fish (3·5 mm.). Similarly the length during the winter non-growing period was about 124 mm. in the Tamar fish as against 132 mm. for the inshore fish in the Clyde.

WEIGHT

Of the herring caught, samples at definite sizes were weighed at intervals throughout the year. The sizes chosen were at approximately 5 mm. intervals over the whole size range in each sample. The fish were usually weighed fresh after removal of adherent moisture and then dried to constant weight at 105° C. The results of the dry weight determinations are shown in Table IV and Fig. 5. It is found that the weights of the inshore herring fall into two groups, (*a*) those of the growing period from July 4 1936 to November 27 1936 and from April 29 1937 to May 27 1937, and (*b*) those of the winter period (in the intervening months) when growth had stopped. The relation between the dry weight in gm. (W) and the length in mm. (L) during the growing period is given by the equation $W = 0{\cdot}000000258L^{3{\cdot}37}$, and during the winter period by $W = 0{\cdot}0000001095L^{3{\cdot}47}$. For adult herring from the English Channel, Fraser (1931) using the wet weight determinations of Orton (1916) found $W = 0{\cdot}00000337L^{3{\cdot}149}$.

For the Clyde inshore herring, the weight of the *fresh* fish fell only slightly during the non-growing period, but the water content was relatively higher and the fat content relatively lower so that there was a fall in dry weight as is seen in Table IV and Fig. 5. When growth began again in the spring, the fat content rose, the water content fell, and the points come once more on the upper curve. Similar conditions in adult herring have been described by Lea (1911). Fig. 6 shows the relationship between the logarithms of the weights and the logarithms of the lengths for growing and non-growing periods. The points obviously lie on two straight lines, the equations for which (given above) were derived by calculation from the data.

The transition from the curve for the growing period to that for the non-growing period is shown in the weights of herring on February 9 (Table IV).

The points representing the weights of the smaller herring lie on or near the upper curve of Fig. 5, while those for the larger herring lie on or near the lower. Thus the larger herring reach winter weight conditions in advance of the smaller herring. Similarly on April 29 the weights of the smaller herring are on or near the lower curve while those of the larger herring approach the upper curve. Thus the larger herring reach summer conditions in advance of the smaller herring.

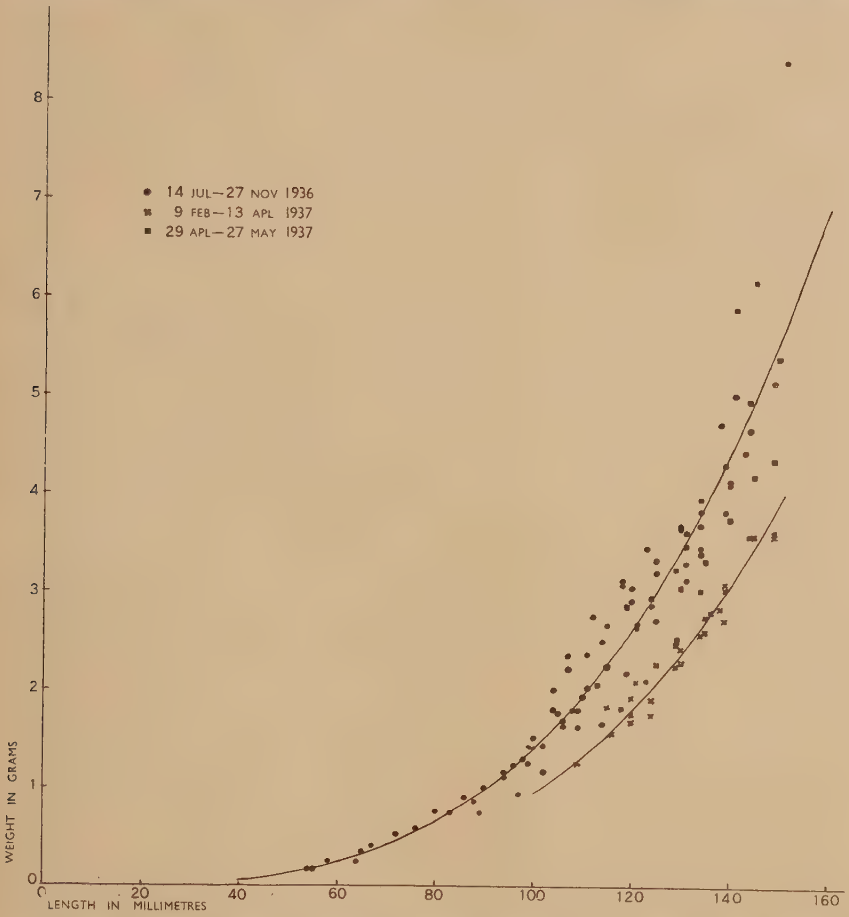


Fig. 5. The relation of weight to length in inshore herring. Upper curve, growing periods; lower curve, non-growing period.

It will be noticed that the growth period according to weight seems to continue for longer than the growth period according to length and that increase in weight begins again in spring before any increase in average length. As will be shown later, this is related to fat storage.

Only a small number of weighings of offshore (Clyde spring-spawned) herring were made and the weight-length relationship found is only slightly different from that for inshore fish (Table IV and Fig. 7). For the growing period the relationship is given by $W=0{\cdot}0000000436L^{3{\cdot}75}$ but for the winter non-growing period the values were lower and the equation is $W=0{\cdot}0000000172L^{3{\cdot}88}$. The offshore fish in the premetamorphosis stage had a weight-length relationship of $W=0{\cdot}0000020L^{4{\cdot}52}$ (Marshall, Nicholls and Orr, 1937).

TABLE IV. LENGTH, WET-WEIGHT AND DRY-WEIGHT MEASUREMENTS

Inshore fish

14. vii. 36			20. vii. 36			27. vii. 36			3 & 4. viii. 36			10. viii. 36			14. viii. 36		
mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.
67	1·95	0·41	58	1·25	0·26	54	0·74	0·18	96	5·41	1·25	94	5·13	1·17	104	8·33	2·01
72	2·48	0·53	65	1·73	0·36	55	0·74	0·17	97	4·70	0·94	96	5·65	1·24	107	10·35	2·36
76	2·79	0·59	99	6·22	1·43	64	1·07	0·25	102	5·72	1·18	99	6·14	1·43	112	10·24	2·76
80	3·46	0·77	104	7·89	1·81				102	6·54	1·44	100	6·33	1·42	118	11·76	3·08
83	3·46	0·76							108	7·72	1·80	105	7·42	1·77			
86	4·03	0·91										107	8·92	2·22			
88	4·09	0·87										109	6·88	1·63			
90	4·44	1·01										114	9·77	2·50			
94	5·14	1·12										115	10·13	2·67			
												118	11·45	3·13			

19 & 24. viii. 36			31. viii. 36			29. ix. 36			5 & 13. x. 36			27. xi. 36			9. ii. 37		
mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.
120	11·92	3·05	89	..	0·76	106	7·62	1·70	124	..	2·87	98	5·54	1·31	115	8·16	1·85
123	13·26	3·46	100	..	1·52	111	8·93	2·03	131	..	3·62	109	7·45	1·80	121	9·82	2·09
125	13·01	3·21	106	..	1·64	121	11·78	2·69	131	..	3·30	114	8·06	1·66	125	11·10	2·27
			110	..	1·94	130	14·42	3·68	134	..	3·69	119	8·46	2·18	129	11·97	2·47
			115	..	2·26	134	15·29	3·46	134	..	3·84	125	11·68	2·72	136	13·66	2·81
			120	..	2·92	138	17·17	4·73	140	..	4·11	131	12·65	3·13	139	15·07	3·09
			125	..	3·33	141	19·32	5·02	140	..	4·14	134	13·82	3·40	145	17·38	3·58
			130	..	3·66				144	..	4·67	139	15·68	3·83			
												143	17·35	4·44			
												149	20·35	5·15			

15. iii. 37			29. iii. 37			13. iv. 37			29. iv. 37			13. v. 37			26 & 27. v. 37		
mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.
109	6·40	1·26	120	9·61	1·93	116	8·16	1·56	113	9·18	2·06	111	9·56	2·37	121	..	2·65
120	8·94	1·76	124	9·68	1·92	120	8·84	1·68	118	8·50	1·82	119	11·53	2·86	129	..	3·24
124	9·97	1·91	130	12·33	2·43	124	9·39	1·75	123	10·32	2·10	124	12·42	2·95	131	..	3·47
130	11·72	2·29	135	13·13	2·60	129	11·52	2·25	129	12·19	2·53	130	13·06	3·05	134	..	3·96
135	13·82	2·75	138	14·48	2·84	134	12·83	2·57	134	14·25	3·02	135	14·57	3·32	141	..	5·90
139	14·89	3·03	149	17·76	3·58	139	14·36	2·72	140	16·67	3·75	139	17·64	4·31	145	..	6·17
144	17·68	3·58							145	18·84	4·19	144	19·54	4·96	151	..	8·42
149	18·04	3·62							149	19·86	4·35	150	22·81	5·40			

Offshore fish

10. viii. 36			26. v. 37			21. iii. 38		
mm.	gm.	gm.	mm.	gm.	gm.	mm.	gm.	gm.
119	10·93	2·76	155	..	7·26	73	1·85	0·33
122	10·87	2·64	160	..	7·40	80	2·26	0·47
124	13·06	3·49	164	..	9·51	85	2·62	0·52
125	12·42	3·09	170	..	10·24	90	3·15	0·65
129	14·73	4·16	175	..	11·76	95	4·09	0·86
131	14·95	3·80	181	..	12·31	100	4·77	0·99
133	14·66	3·70	185	..	13·17	105	5·66	1·15
139	16·89	4·28	190	..	15·66	110	6·92	1·46
140	18·34	4·81				115	7·47	1·60
144	18·57	4·78				119	9·11	1·94
145	21·36	6·25				126	10·24	2·32

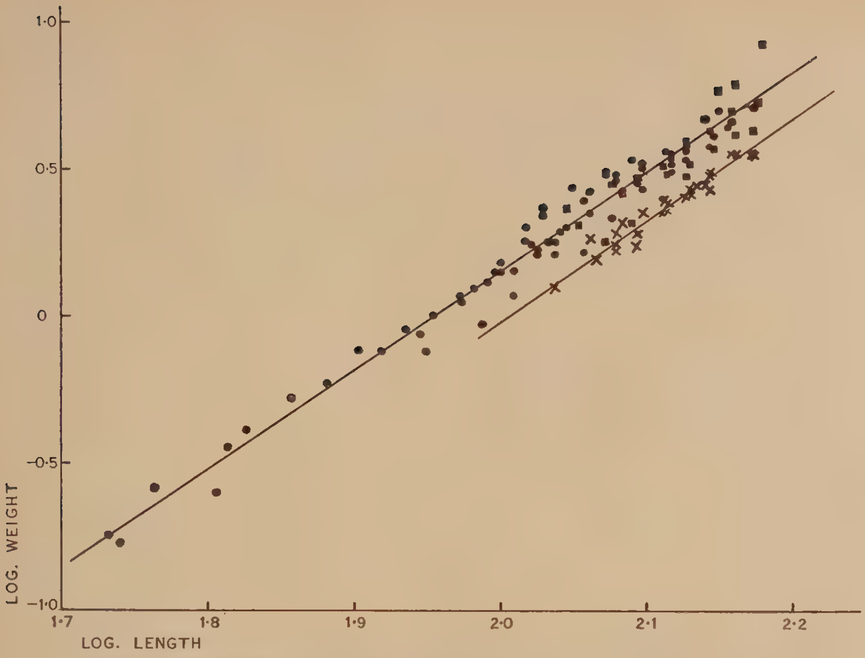


Fig. 6. Relation of logarithm of weight to logarithm of length in inshore herring. Upper curve, growing periods; lower curve, non-growing period. The points are the same as in Fig. 5.

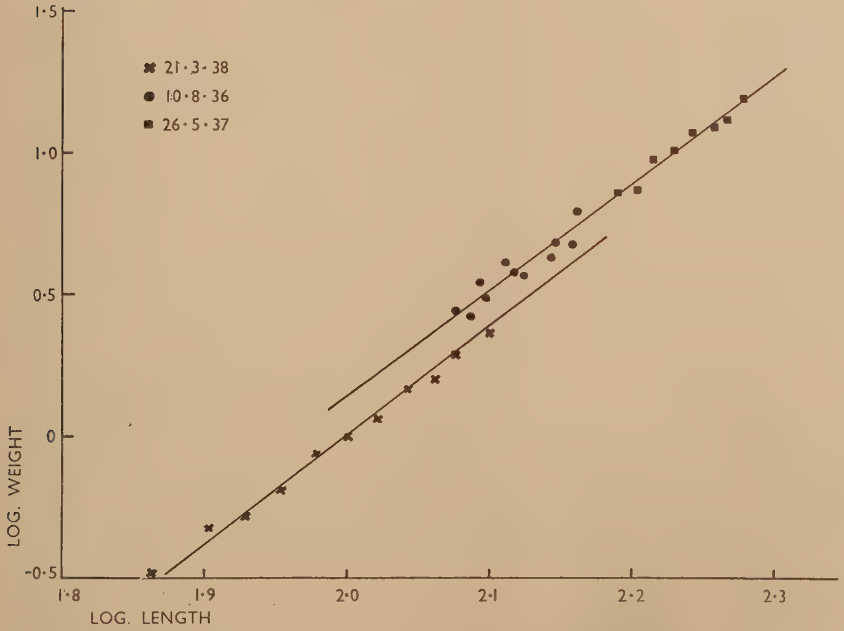


Fig. 7. The relation of logarithm of weight to logarithm of length in offshore herring. Upper curve, growing period; lower curve, non-growing period.

CHEMICAL COMPOSITION

From the catches of inshore herring a sample of fish of about the average size for the catch was dried to constant weight at 105° C. and used for determination of protein, fat and ash. Protein was determined by the Kjeldahl method, fat by the Soxhlet ether extraction method and ash by ignition. The results are shown in Table V and Fig. 8.

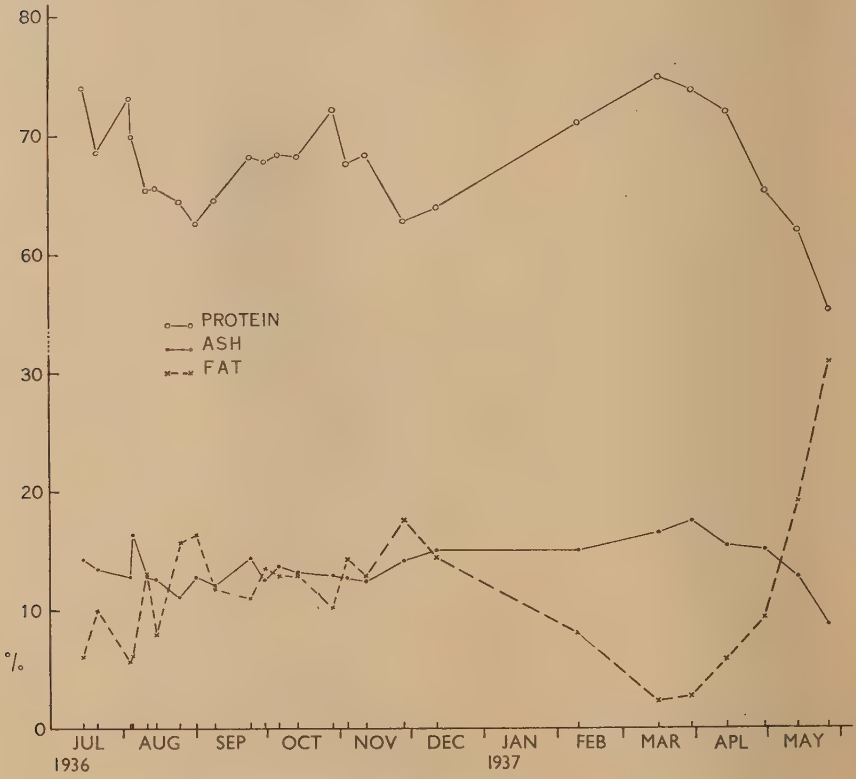


Fig. 8. Percentage chemical composition of inshore herring.

The fat content varied from 2 to 30%. During the growing period it was irregular with a tendency to increase up till the end of November when it was about 17%. This is at least 4 weeks after growth in length had ceased, which suggests that fat was being stored for utilization during the winter. Similarly although fat was increasing from the middle of March onwards, showing that the fish were recuperating, there was no increase in length until May. During the winter only a few analyses were made. By February the fat content had fallen considerably and its lowest value was reached on March 15 when it was about 2%. Thereafter there was a steady and rapid increase up to 30% at the end of May.

The minor irregularities in the fat results may be due to some extent to the size of the fish used in the sample. On August 10 1936, when the size range was considerable, analyses were made on fish of different size ranges. The results (Table V) show that the fat percentage increased with increasing size of fish.

TABLE V. CHEMICAL COMPOSITION

Date	Size mm.	Dry weight		
		Protein %	Fat %	Ash %
14. vii. 36	80–90	74·01	6·15	14·33
20. vii. 36	90–100	68·56	9·94	13·52
3. viii. 36	90–100	73·13	5·69	12·80
4. viii. 36	90–100	69·88	6·15	16·38
10. viii. 36	100–110	65·35	13·16	12·76
10. viii. 36	110–120	61·70	16·72	12·98
*10. viii. 36	120–130	60·30	21·17	12·04
*10. viii. 36	130–140	57·37	25·42	12·65
14. viii. 36	100–110	65·57	7·90	12·63
24. viii. 36	..	64·52	15·71	11·13
31. viii. 36	120–130	62·62	16·41	12·83
8. ix. 36	120–130	64·57	11·81	12·12
23. ix. 36	120–130	68·18	11·04	14·43
29. ix. 36	135–140	67·82	13·55	12·51
5. x. 36	130–140	68·37	12·89	13·70
13. x. 36	130–140	68·21	12·88	13·16
28. x. 36	130–140	72·06	10·18	12·90
3. xi. 36	130–140	67·61	14·35	12·71
11. xi. 36	120–130	68·26	12·88	12·39
27. xi. 36	130–140	62·82	17·61	14·13
11. xii. 36	130–140	63·92	14·48	14·99
9. ii. 37	130–140	70·98	8·10	15·03
15. iii. 37	130–140	74·85	2·36	16·48
29. iii. 37	130–140	73·78	2·75	17·49
13. iv. 37	130–140	71·98	5·86	15·40
29. iv. 37	130–140	65·40	9·38	15·13
13. v. 37	135–145	62·04	19·22	12·77
26. v. 37	160–170	55·32	30·90	8·82

* Offshore, 1-ring herring.

The protein content varied from 55 to 74% and its fluctuations correspond inversely to those of the fat content. As has been mentioned above, the fall in fat content in winter is accompanied by an increase in water content so that the wet weight and weight of protein change comparatively little.

In Table VI and Fig. 9 are shown the calculated weight and composition of the average inshore herring during its first year. The lengths and weights were obtained from the curves in Figs. 3 and 5 with interpolations for the change from summer to winter composition. The chemical composition was calculated from the results given in Table V.

The analyses of the chemical composition of the inshore herring show much the same type of seasonal fluctuation as has been found for herring muscle by Bruce (1924), Channon & el Saby (1932), and by Lovern & Wood (1937). The last authors found a minimum fat content in April of about 2–3 % which is the same as that of the inshore fish in March. This low value is found at the end of the winter period of poor plankton. The maximum value found for fat by Lovern & Wood (over 20 %) is lower than the maximum found in inshore fish (31 %), but agrees in that it occurred at the time when food was abundant both in the plankton (spring) and in the herring guts

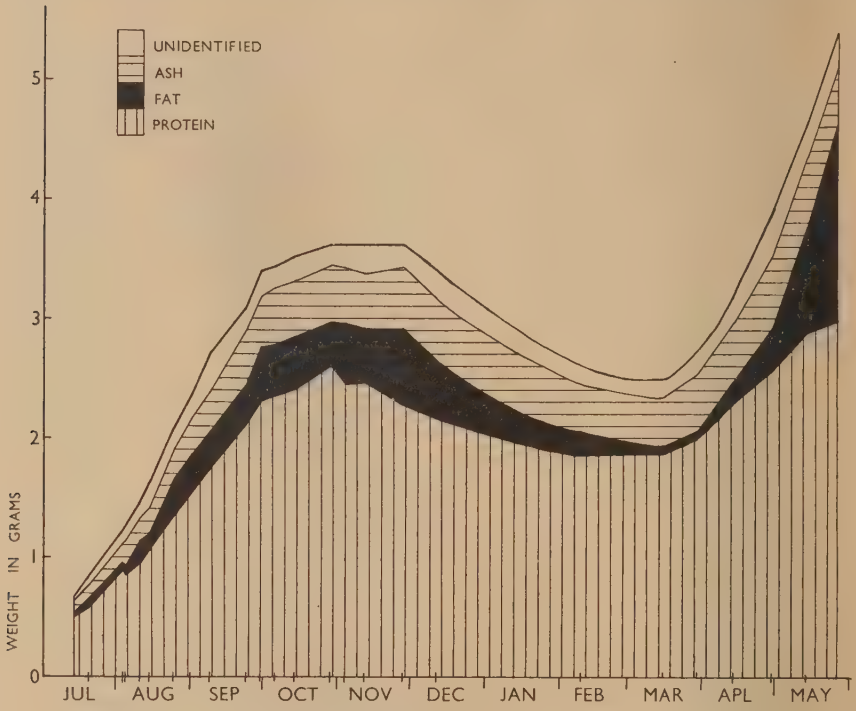


Fig. 9. Dry weight and chemical composition of the average inshore herring.

(Table VII and Fig. 10). Similarly for spring-spawning herring, Lovern & Wood found values generally high during the summer with a slight additional rise in the late autumn (maximum in December). The fat values for inshore fish remained high during the summer and did not fall till December or later. A close comparison of the results obtained on the young Clyde fish (inshore type) with those of other workers is not possible for two reasons; firstly, in the fish analysed in the present report the whole fish was used and not either the muscle or separate organs; secondly, the influence of the state of sexual maturity on the fat content of different tissues of adult herring is important.

It would have been desirable to remove the gut contents before analysis, but this omission is likely to have had only a very small effect. In the most striking case where food was abundant and consisted chiefly of *Calanus*, it is possible to calculate the effect of the inclusion of the gut contents. Each fish on May 26 1937 contained on an average almost 2000 *Calanus* and since the composition of *Calanus* is known (Marshall, Nicholls & Orr, 1934) it can be calculated that the gut contents accounted for about 0·06 gm. fat, i.e. only about 1% of the fat in the fish is represented by the *Calanus* in the gut. At other times the food in the gut is negligible from this aspect.

TABLE VI. COMPOSITION OF AVERAGE HERRING

Date	Av. length mm.	Av. wt. gm.	Protein gm.	Fat gm.	Ash gm.
14. vii. 36	80	0·67	0·50	0·04	0·10
20. vii. 36	86	0·85	0·58	0·08	0·11
3. viii. 36	96	1·22	0·89	0·07	0·16
4. viii. 36	96	1·22	0·85	0·08	0·20
10. viii. 36	101	1·46	0·95	0·19	0·19
14. viii. 36	104	1·63	1·07	0·13	0·21
24. viii. 36	112	2·07	1·34	0·32	0·23
31. viii. 36	116	2·35	1·47	0·39	0·30
8. ix. 36	121	2·70	1·74	0·32	0·33
23. ix. 36	126	3·09	2·11	0·34	0·45
29. ix. 36	129	3·39	2·30	0·46	0·42
5. x. 36	130	3·43	2·34	0·44	0·47
13. x. 36	131	3·52	2·40	0·45	0·46
28. x. 36	132	3·61	2·60	0·37	0·47
3. xi. 36	132	3·61	2·44	0·52	0·46
11. xi. 36	132	3·61	2·46	0·46	0·45
27. xi. 36	132	3·61	2·27	0·64	0·51
11. xii. 36	132	(3·38)	2·16	0·49	0·51
9. ii. 37	132	(2·60)	1·85	0·21	0·39
15. iii. 37	132	2·50	1·87	0·06	0·41
29. iii. 37	132	(2·70)	1·99	0·07	0·47
13. iv. 37	132	(3·18)	2·29	0·19	0·49
29. iv. 37	135	3·91	2·56	0·37	0·59
13. v. 37	142	4·63	2·87	0·89	0·59
26. v. 37	156	5·38	2·98	1·66	0·47

Values in brackets are interpolated.

FOOD AND ITS RELATION TO THE PLANKTON

When a catch of herring was taken, a number of fish was immediately preserved in formalin for food examination. From ten of these the guts were removed, opened, and the contents mixed. The volume of this was measured after settlement and a subsample was then examined and all recognizable organisms counted. When the fish were small or the guts nearly empty, a larger number was used, but the results are always expressed as the number of organisms per fish. They are shown in Table VII and Fig. 10. The numbers of herring used are of course too small for accurate quantitative work, but the results give a good indication of the type of food being eaten.

Table VII. Food of Inshore Herring

Date	Volume c.c.	*Calanus*		Harpacticoid copepods		Other copepods		Cladocera		Ostracods and cirripedes		Cyphonautes		Molluscan larvae		Other organ-isms	Total no.	Notes
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%			
14. vii. 36	..	..	..	2452	90·4	238	9·0	2	0·1	5	0·2	..	..	1	0·1	13	2711	3 amphipods
20. vii. 36	0·5	146	15·1	74	7·6	459	47·5	246	25·4	9	0·9	2	0·2	22	2·3	11	967	..
27. vii. 36	0·4	..	..	71	13·2	213	39·4	102	18·9	8	1·5	64	11·9	70	13·0	12	540	..
3. viii. 36	0·7	4	0·2	9	0·5	988	56·8	699	40·2	13	0·7	9	0·5	14	0·8	2	1738	..
10. viii. 36	1·3	453	31·6	3	0·2	504	35·2	413	28·8	6	0·4	20	1·4	13	0·9	23	1434	12 polychaete larvae
14. viii. 36	0·5	8	1·7	146	30·2	99	20·4	54	11·2	34	7·0	117	24·2	19	3·9	7	484	..
24. viii. 36	0·6	1	0·1	9	0·5	176	9·4	6	0·3	22	1·2	1643	88·2	7	0·4	..	1864	..
31. viii. 36	1·05	1	0·3	3	1·0	207	69·0	11	3·7	4	1·3	64	21·3	1	0·3	8	300	..
8. ix. 36	0·9	1	0·1	7	0·9	592	73·6	9	1·1	5	0·6	114	14·2	15	1·9	61	804	61 polychaete larvae
15. ix. 36	0·7	..	..	2	0·1	165	5·3	11	0·4	12	0·4	2896	93·2	19	0·6	4	3109	..
*21. ix. 36	1·3	635	65·3	..	..	310	31·9	..	..	..	..	..	..	..	..	30	973	24 *Oikopleura*
23. ix. 36	0·55	..	..	3	0·7	405	94·2	6	1·4	1	0·2	9	2·1	1	0·2	5	430	..
29. ix. 36	0·55	..	..	9	2·7	317	95·5	1	0·3	..	..	..	..	..	..	5	332	..
5. x. 36	0·7	27	6·6	1	0·2	324	79·9	2	0·5	2	0·5	47	11·6	1	0·2	2	406	..
13. x. 36	1·1	435	39·6	..	..	467	42·6	18	1·6	6	0·5	3	0·3	1	0·1	168	1097	2 *Zoeae*; 3 *Megalopa*; 2 mysids; 2 *Sagitta*; 155 *Oikopleura*
28. x. 36	0·8	12	2·5	2	0·4	405	89·4	5	1·1	..	..	8	1·8	1	0·2	20	453	4 amphipods; 5 *Zoeae*
3. xi. 36	0·6	46	35·7	4	3·1	73	56·6	..	..	1	0·8	1	0·8	2	1·6	2	129	..
13. xi. 36	1·8	575	74·3	..	..	194	25·1	..	..	..	..	..	..	..	..	5	774	1 euphausid; *Sagitta* present
27. xi. 36	0·45	22	38·6	2	3·5	32	56·1	..	..	..	..	..	..	..	..	1	57	..
11. xii. 36	0·2	1	3·7	..	..	24	88·9	..	..	..	..	..	..	..	..	3	27	..
28. xii. 36	0·25	1	2·6	1	2·6	35	92·2	..	..	..	..	..	..	..	..	1	38	1 *Sagitta*
13. i. 37	0·6	28	49·1	..	..	16	28·1	..	..	..	..	..	..	..	..	13	57	11 *Sagitta*; 1 amphipod
9. ii. 37	0·8	66	80·5	2	2·4	9	11·0	..	..	..	..	..	..	..	..	4	82	Remains of fish larva; *Sagitta* present
†1. iii. 37	0·6	40	57·1	1	1·4	9	12·9	..	..	..	..	..	..	..	..	18	70	4 amphipods; 10 *Cumacea*; 1 mysid; remains of fish larva and *Sagitta*
15. iii. 37	0·45	12	27·9	5	11·6	12	27·9	..	..	..	..	..	..	..	..	13	43	8 amphipods; 5 *Cumacea*; remains of *Sagitta*
29. iii. 37	0·5	1	0·8	20	15·9	11	8·7	..	..	83‡	65·9	..	..	..	..	11	126	‡All cirripede nauplii
13. iv. 37	0·8	60	10·0	6	1·0	94	15·7	..	..	426‡	71·2	..	..	1	0·2	10	598	‡215 cirripede nauplii; 211 cyprids
29. iv. 37	0·9	5	0·4	8	0·6	21	1·6	..	..	1286‡	97·4	..	..	..	..	1	1321	‡104 cirripede nauplii; 1182 cyprids
13. v. 37	1·3	317	67·4	3	0·6	124	26·4	4	0·9	14	3·0	..	..	..	..	8	470	..
†26. v. 37	3·75	1856	92·0	9	0·4	132	6·6	11	0·5	2	0·1	..	..	..	..	7	2017	..
27. v. 37	2·0	521	61·6	49	5·8	241	28·5	21	2·5	4	0·5	..	..	..	..	9	845	..
31. v. 27	0·7	26	4·4	347	58·2	113	19·0	75	12·6	3	0·5	..	..	2	0·3	30	596	12 mysids; 12 decapod larvae
11. viii. 37	0·6	1	0·2	1	0·2	627	98·8	..	..	..	..	..	..	..	..	4	634	..

* Drift nets.

† Sprat ring net.

During the growing period both in summer 1936 and spring 1937, the gut contents of the inshore fish varied considerably both in volume and composition; in the winter the majority of the guts were almost empty.

For most of the year copepods formed the bulk of the food, but in spring and summer, at times when other organisms were common in the plankton, an individual catch might show these in abundance. Thus during August and September Cyphonautes (polyzoan larvae) were common and on September 15 rose to 93 % of the total numbers. In spite of their large numbers, however, they are relatively unimportant as food because of their small size. On September 15 when 2896 Cyphonautes were present the total volume of the food was only 0·7 c.c. In spring cirripede larvae, both nauplii and cyprids, were abundant and on April 29 formed 97·4 % of the food. Cirripede larvae and Cyphonautes were the most important organisms occurring sporadically, but, as may be seen in Table VII, euphausids, Cladocera, *Sagitta*, and *Oikopleura* all appeared at times. Occasionally a few *Chironomus* larvae were ingested.

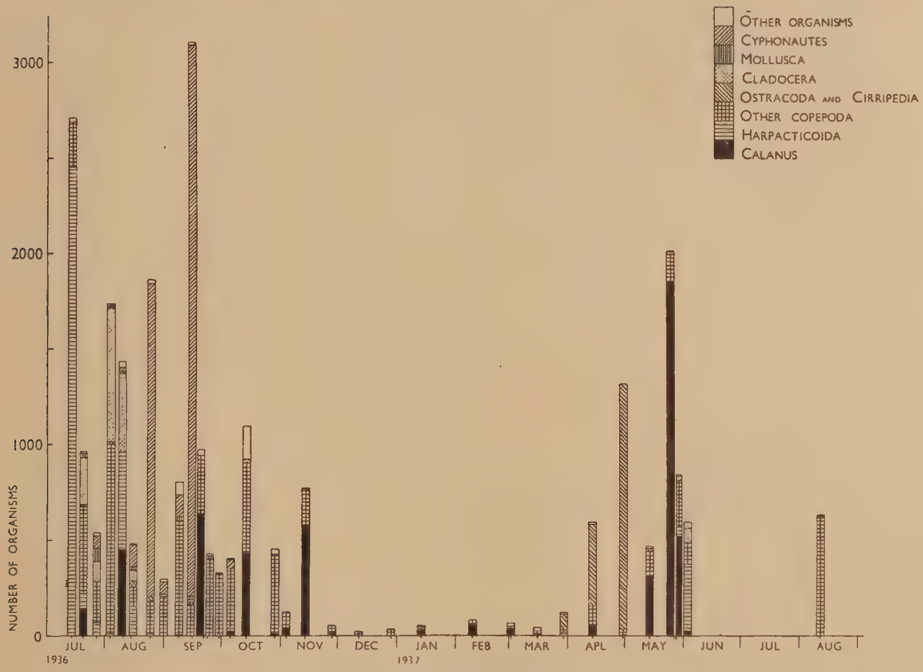


Fig. 10. Composition of the food of inshore herring.

Of the copepods *Calanus*, although not the most numerous, was certainly the most important owing to its large size. In Fig. 11 which shows the volume of the gut contents each of the peaks, with the exception of that on August 31, is due to the presence of *Calanus*. In May when the herring were increasing rapidly in weight and fat content, they were feeding mainly on *Calanus* and on May 26 there were 1856 *Calanus* per gut. The other copepods were most numerous from July to October, *Pseudocalanus*, *Microcalanus*, and *Acartia* appearing for longer than *Centropages*, *Temora*, and *Oithona*. All disappeared almost completely during the winter to reappear again in May. In July to August 1936 and in May 1937 harpacticoid copepods were common and on one occasion, July 14, each gut contained on the average 2452, forming 90% by number of the food organisms. They were mostly littoral forms, e.g. *Dactylopusia* and other thalestrids, showing that the herring were feeding inshore.

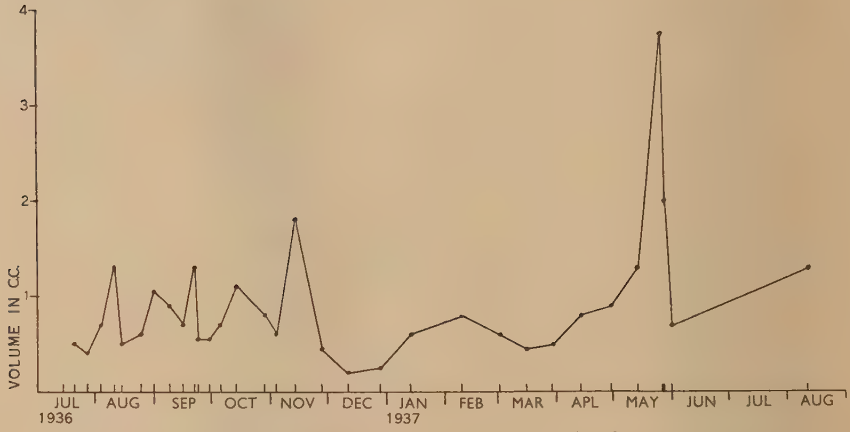


Fig. 11. Volume of the food of inshore herring.

On August 14–15 when herring were caught at 2 hr. intervals during the night, a sample of the guts was examined from each catch (Table VIII and Fig. 12). The volume of the food was never large but was highest from 7–11 p.m. and lowest from 1–5 a.m. Copepods were the most numerous organisms in the catch at 5 p.m. when there were over 1000 harpacticoids per gut. In the catches from 7–11 p.m. *Centropages*, *Temora*, Cladocera, cirripede larvae, and Cyphonautes formed the bulk of the food, as they did also in the later catches, although very much less numerous. It was hoped to find out if the fish came inshore to feed and at what time during the night they fed most, but from this point of view the results were disappointing. The harpacticoids in the first catch indicate that they had been feeding inshore, but in this, as in all catches, most of the food was in the intestine and little in the stomach which suggests that they were not feeding at the time they were caught.

A comparison of the volume of the gut contents with the growth curve for the herring and their chemical composition shows general agreement (Figs. 11, 3 and 8). When the volume of the food was high during the summer of 1936 and the spring of 1937, the herring were growing. During the winter period when food was scarce, growth had stopped and the fish were losing fat. Although growth had stopped by the middle of October, the volume of the food was still considerable and it has been shown that it was being used partly for fat storage; similarly the food showed an increase in spring some time before any increase in length began, correlated with the replacement of fat lost in winter.

Only six samples of offshore (Clyde spring-spawned) fish were examined and they showed little difference from the inshore fish in their food except that there was a reduction in the number of harpacticoid copepods.

TABLE VIII. FOOD OF HERRING DURING NIGHT OF AUGUST 14–15 1936

Time	No. of herring	Volume of food in c.c.	*Calanus* no.	Harpacticoid copepods no.	Other copepods no.	Cladocera no.	Ostracods and cirripedes no.	Cyphonautes no.	Molluscan larvae no.	Other organisms no.	Total no.
5 p.m.	132	0·5	..	1063	203	103	124	438	25	14	1970
7 p.m.	4500	0·7	43	9	144	140	53	65	45	10	509
9 p.m.	>10000	0·7	4	3	192	114	33	30	16	12	404
11 p.m.	450	0·7	7	21	97	40	22	340	10	9	546
1 a.m.	10	0·3	..	34	29	14	20	11	14	7	129
3 a.m.	12	0·3	..	31	45	6	11	23	17	5	138
5 a.m.	293	0·25	..	1	8	1	..	9	4	..	23
7 a.m.	6	0·45	13	8	71	17	5	20	15	5	154

When a catch of herring was made, a tow-netting was taken in the same place. A 5 minute haul was made with a 40 cm. fine silk net at about 1 m. below the surface and all organisms counted after preservation in formalin. The results are given in Table IX, in which the organisms are grouped as in Table VII to assist comparison. The figures for August 14 1936 are averages based on all the hauls taken during the night of August 14–15. The object was to compare the plankton with the food in the herring guts.

As might be expected, the plankton hauls were poor during the winter period and rich during the spring and summer but, apart from this general relationship, the comparison with the contents of the herring guts is disappointing. The reason for the poor agreement between plankton hauls and gut contents is probably that on the majority of occasions the herring had been feeding offshore, whereas the tow-nettings were taken inshore where the herring were actually captured.

The most striking agreement was from March 29 to April 29 when cirripede larvae, first as nauplii and then as cyprids, were abundant both in the tow-nettings and in the food. *Oikopleura* was common in both on September 21 and October 13. Cladocera were represented seasonally in the guts according to their appearance in the plankton, as was also Cyphonautes. With animals like the last, which occur in swarms, it is largely a matter of chance whether they are richly represented in the catch or not. Although Cyphonautes was

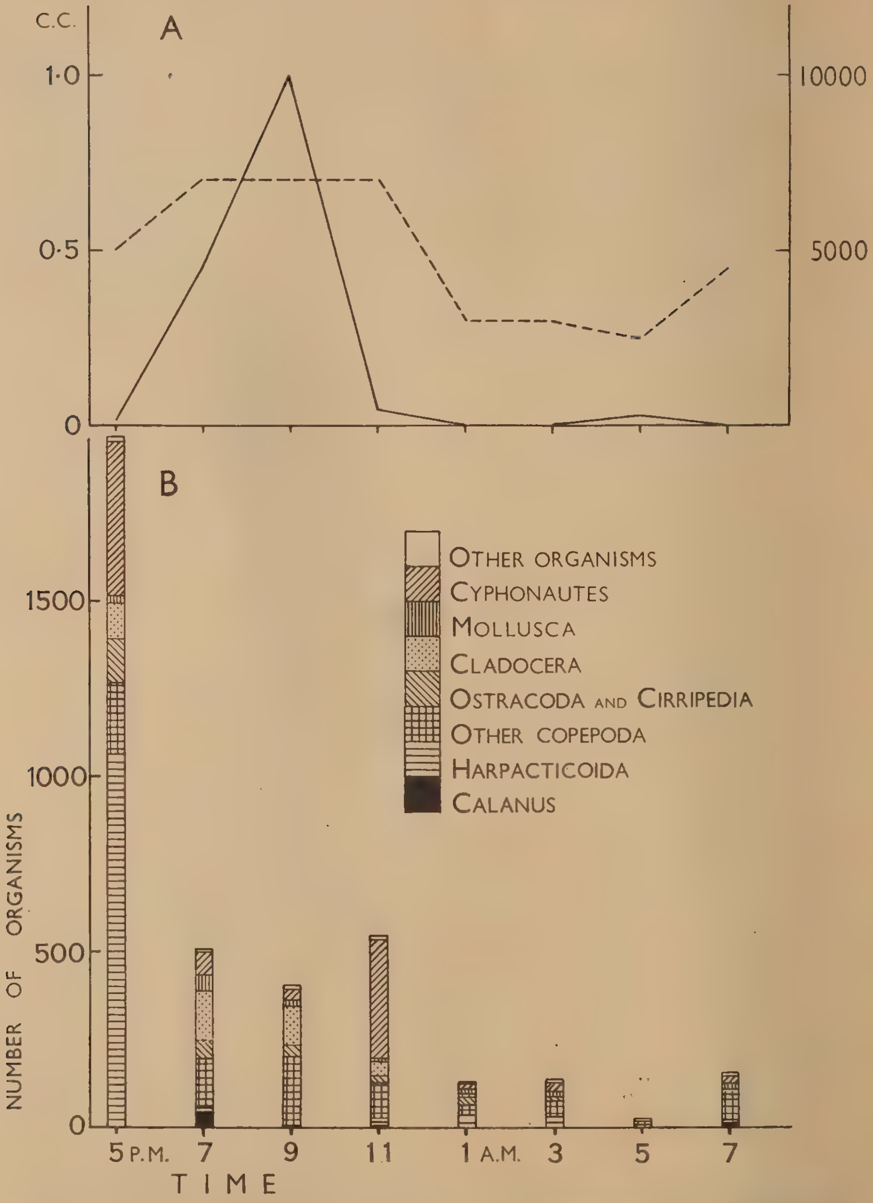


Fig. 12. A, approximate number of herring per haul (continuous line) and volume of food per herring (broken line) from 5 p.m. to 7 a.m. August 14–15 1936. B, composition of the food over the same period.

TABLE IX. PLANKTON

Date	*Calanus*		Harpacticoid copepods		Other copepods		Cladocera		Ostracods and cirripedes		Cyphonautes		Molluscan larvae		Other organisms		Total no.	Notes
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%		
†18. vii. 36	160	2·0	160	2·0	5400	68·5	460	5·8	110	1·4	10	0·1	540	6·9	1040	13·2	7880	670 polychaete larvae; no amphipods
28. vii. 36	..	..	180	1·7	3990	38·2	90	0·9	..	..	390	3·7	4440	42·5	1350	12·9	10440	900 echinoderm larvae; 450 polychaete larvae
4. viii. 36	..	..	280	3·5	3000	37·1	3080	38·1	80	9·9	200	2·5	730	9·0	720	8·9	8090	380 polychaete larvae
10. viii. 36	..	..	1050	17·0	4150	67·4	150	2·4	210	3·4	70	1·1	100	1·6	430	7·0	6160	290 polychaete larvae
14. viii. 36	2	0·0	163	1·7	4214	43·6	464	4·8	307	3·2	1161	12·0	3019	31·2	334	3·5	9662	..
19. viii. 36	10	0·8	320	26·2	140	11·5	..	..	30	2·5	10	0·8	400	32·8	310	25·4	1220	140 polychaete larvae
24. viii. 36	..	..	130	3·0	2985	69·7	30	0·7	145	3·4	80	1·9	545	12·7	365	8·5	4280	230 polychaete larvae
31. viii. 36	4	0·3	70	5·2	470	35·0	78	5·8	4	0·3	8	0·6	88	6·6	622	46·3	1344	550 *Oikopleura*
8. ix. 36	..	..	90	1·9	3590	77·7	40	0·9	40	0·9	150	3·2	420	9·1	290	6·3	4620	170 polychaete larvae
15. ix. 36	10	0·3	55	1·5	2735	75·3	15	0·4	10	0·3	140	3·9	125	3·4	540	14·9	3630	215 *Oikopleura*
23. ix. 36	40	0·1	60	0·1	9940	22·6	40	0·1	20	0·0	60	0·1	3740	8·5	30060	68·4	43960	28000 Rotifers; 1460 *Oikopleura*
29. ix. 36	10	0·1	440	4·8	4760	52·0	20	0·2	..	..	..	..	2590	28·3	1328	14·5	9148	420 *Cumacea*; 360 *Oikopleura*; 350 polychaete larvae
5. x. 36	..	..	580	17·3	2590	77·3	..	..	50	1·5	..	..	80	2·4	50	1·5	3350	..
14. x. 36	..	..	600	4·2	6420	44·9	270	1·9	..	..	..	..	390	2·7	6600	46·2	14280	5100 Rotifers; 600 Turbellaria; 390 *Oikopleura*; 390 polychaete larvae; no decapods, mysids nor *Sagitta*
28. x. 36	..	..	310	6·4	3420	70·5	10	0·2	10	0·2	100	2·1	450	9·3	550	11·3	4850	240 polychaete larvae; no amphipods nor decapods
3. xi. 36	..	..	60	2·1	1600	55·1	..	..	1	0·0	15	0·5	255	8·8	971	33·5	2902	610 polychaete larvae
11. xi. 36	3	0·1	45	1·2	2410	61·7	..	..	..	..	10	0·3	1015	26·1	408	10·5	3891	370 polychaete larvae; 10 *Sagitta*; no euphausids
27. xi. 36	20	0·6	65	1·9	2470	70·5	5	0·1	5	0·1	..	..	760	21·7	180	5·1	3505	90 polychaete larvae
11. xii. 36	..	..	2	0·9	194	88·9	..	..	..	..	..	..	..	..	22	10·1	218	16 *Cumacea*
28. xii. 36	6	0·4	30	2·0	1274	85·0	..	..	..	..	2	0·1	142	9·5	44	2·9	1498	34 polychaete larvae; 2 *Sagitta*
13. i. 37	5	1·6	17	5·3	122	38·2	..	..	..	..	..	..	49	15·4	126	39·5	319	93 Rotifers; 5 amphipods; no *Sagitta*
9. ii. 37	10	5·8	6	3·5	67	38·7	..	..	2	1·2	..	..	57	33·0	31	17·9	173	No fish larvae nor *Sagitta*
15. iii. 37	..	..	90	9·6	342	36·4	..	..	326*	34·7	4	0·4	94	10·0	84	9·0	940	*324 cirripede larvae; 64 polychaete larvae; amphipods, *Cumacea* and *Sagitta* present
29. iii. 37	2	0·3	10	1·5	70	10·4	..	..	501*	74·2	..	..	18	2·7	74	11·0	675	*All cirripede nauplii; 66 polychaete larvae
†13. iv. 37	6340	25·6	..	..	3640	14·7	60	0·2	12340*	49·7	..	..	60	0·2	2360	9·5	24800	*All cirripedes, mainly nauplii; 1680 *Oikopleura*
29. iv. 37	54	3·6	105	7·0	66	4·4	16	1·1	1074*	72·0	..	..	3	0·2	174	11·7	1492	*All cirripedes, mainly cyprids; 77 polychaete larvae
13. v. 37	202	4·8	82	2·0	1066	25·5	1334	31·9	712	17·0	4	0·1	332	7·9	456	10·9	4188	252 euphausid larvae
27. v. 37	6	0·4	312	19·8	548	34·8	290	18·4	30	1·9	..	..	353*	22·4	34	2·2	1573	*Mainly *Littorina* eggs

† Offshore hauls.

not obtained on the dates they occurred in the herring guts, additional tow-nettings taken in Kames Bay about the same time showed that they were abundant. Among the herring also not all the guts contained Cyphonautes, but in four out of ten the intestine was packed with them.

The most marked disagreement is in the numbers of *Calanus*, which was frequently common in the guts and quite absent from the plankton hauls. This suggests that the herring had been feeding offshore before they were caught although the presence of typical littoral plankton, e.g. harpacticoids, shows that they fed inshore as well. On only one occasion was *Calanus* abundant in the tow-nettings and that was when the haul was taken further off shore than usual.

Much has been written on the food of the herring, but it has been mainly concerned with adult fish. In general it is agreed that herring on the west coast of Scotland depend more upon copepods and euphausids than do those on the east coast (Scott, 1907) which have a larger proportion of young fish (mainly *Ammodytes*) in their diet (Hardy, 1924; Savage, 1937). The food of young herring about 50–150 mm. in length is dealt with in papers by Hardy (1924), Jespersen (1928), Wailes (1936), and Battle *et al.* (1936).

In general our results are in good agreement with theirs. Copepods form the chief part of the diet and other organisms appear seasonally. Hardy, (1924) dealing with whitebait herring in the Thames estuary, found copepods, chiefly *Pseudocalanus*, *Temora*, and *Eurytemora* common, harpacticoids numerous at times, and cyprid larvae of cirripedes important in spring and autumn. Ogilvie (1934) mentions that harpacticoids, though rare in adult herring, are frequent in young herring. Jespersen's (1928) young herring of 6–14 cm. were caught only in the winter half-year but they were then feeding voraciously, mainly on copepods (*Temora*, *Pseudocalanus* and *Paracalanus*). He found that non-crustaceous food was more important for young than for adult fish. Cyphonautes, however, was rarely taken although common in the plankton from February to March, which contrasts with our results. Another contrast is that his herring (adults in this case) appeared to select cirripede cyprids even when the nauplii were more abundant, whereas ours took both in large quantities according to their abundance in the plankton.

Only a few records are available of the fluctuations in the gut contents over the day. Jespersen (1928) compared the quantity of food and the numbers of copepods per fish in samples of young herring from the west coast of Denmark and found that feeding decreased during the night, i.e. from 10 p.m. till 10 a.m. Lissner (1925) dealing with adult herring in the North Sea concluded that they are attracted by a weak light, begin to feed in the afternoon and stop towards morning. Mužinić (1931) found that feeding was at its maximum from about 5 p.m. to 9 p.m. and then slackened off till 4 or 5 a.m. when there was a slight increase. This compares well with the feeding of the inshore herring from the Clyde (Fig. 12 A). Battle *et al.* (1936) state that young herring require a good light to feed by and that although moonlight is bright enough, starlight is not. For this reason the plankton present in the surface waters is most important for them.

We wish to thank the staff of the laboratory for their co-operation in the work. We are indebted to the Fishery Board for Scotland for the loan of a shore seine and for the herring reports obtained through their Fishery Officers in the Clyde; also to the Fisheries Laboratory, Lowestoft, for the loan of a shore seine and drift nets.

SUMMARY

Two groups of young herring are found in the Clyde. One, the offshore group, has been identified as Clyde spring-spawned herring; the other, the inshore type, is of unknown origin. The former were caught only occasionally, the latter at fairly regular intervals during their first year.

The two groups are distinguished by differences in size and identified as belonging to different races by vertebral counts. There was no intermixture.

The offshore herring which metamorphosed at the end of May when 40–50 mm. long, reached a length of 90–100 mm. in winter. The inshore fish which were about 50 mm. long in May reached a length of about 130 mm. in winter.

Equations are given showing the relation between length and weight for inshore and offshore herring during the growing and non-growing periods.

Determinations were made of water, fat, protein and ash content of inshore herring. The fat content rises during the summer and falls in winter. It varies inversely with the water content. The fat content continues to increase for some weeks after growth in length has stopped in winter and rises also in spring some time before increase in length begins again.

The food was examined throughout the year and compared with plankton hauls. It consisted mainly of copepods although other organisms were common at times when abundant in the plankton.

A series of hauls made over a night showed that herring were most abundant inshore at dusk and dawn and contained most food from 7–11 p.m.

REFERENCES

Battle, H. I., Huntsman, A. G., Jeffers, A. M., Jeffers, G. W., Johnson, W. H. & McNairn, N. A., 1936. Fatness, digestion and food of Passamaquoddy young herring. *Journ. Biol. Board Canada*, Vol. II, pp. 401–29.

Bruce, J. R., 1924. Changes in the chemical composition of the tissues of the herring in relation to age and maturity. *Biochem. Journ.*, Vol. XVIII, pp. 469–85.

Channon, H. J. & el Saby, M. K., 1932. Fat metabolism of the herring. I. A preliminary survey. *Biochem. Journ.*, Vol. XXVI, pp. 2021–34.

Ford, E., 1928*a*. Herring investigations at Plymouth. I. Methods of collection and treatment of data. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 237–66.

FORD, E., 1928*b*. Ibid. III. The Plymouth winter fishery during the seasons 1924–25, 1925–26, and 1926–27. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 279–304.

—— 1928*c*. Ibid. IV. The growth of young herrings in the neighbourhood of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 305–19.

—— 1933. The "number of vertebrae" in the herring and its variation. *Journ. Cons. Int. Explor. Mer.*, Vol. VIII, pp. 211–22.

—— 1937. Vertebral variation in teleostean fishes. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 1–60.

FRASER, J. H., 1931. On the size of *Urosalpinx cinerea* (Say) with some observations on weight-length relationship. *Proc. Malacol. Soc.*, Vol. XIX, pp. 243–54.

HARDY, A. C., 1924. The herring in relation to its animate environment. Part I. The food and feeding habits of the herring with special reference to the east coast of England. *Min. Agric. Fish., Fish. Invest.*, Ser. II, Vol. VII, No. 3, pp. 1–53.

JESPERSEN, P., 1928. Investigations on the food of the herring in Danish waters. *Medd. fra Komm. for Havunders., Ser. Plankton*, Vol. II, No. 2, pp. 1–150.

JOHANSEN, A. C., 1919. On the large spring-spawning sea herring (*Clupea harengus* L.) in the north-west European waters. *Medd. fra Komm. for Havunders., Ser. Fisk*, Vol. V, No. 8, pp. 1–56.

KÄNDLER, R., 1932. Unsicherheiten bei Bestimmung der Wirbelzahl infolge Verwachsungserscheinungen. *Journ. Cons. Int. Explor. Mer.*, Vol. VII, pp. 373–85.

LEA, E., 1910. On the methods used in herring investigations. *Cons. Int. Explor. Mer., Publ. de Circ.*, No. 53, pp. 7–174.

—— 1911. A study on the growth of herrings. *Cons. Int. Explor. Mer., Publ. de Circ.*, No. 61, pp. 35–48.

LISSNER, H., 1925. Die Nahrungsaufnahme beim Hering. *Ber. Deutsch. wiss. Komm. f. Meeresf.*, N.F., Bd. I, pp. 199–208.

LOVERN, J. A. & WOOD, H., 1937. Variations in the chemical composition of herring. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 281–93.

MARSHALL, S. M., NICHOLLS, A. G., & ORR, A. P., 1934. On the biology of *Calanus finmarchicus*. V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933, and their relation to the phytoplankton. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 793–828.

—— —— —— 1937. On the growth and feeding of the larval and post-larval stages of the Clyde herring. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 245–67.

MEYER, H. A., 1878. Beobachtungen über das Wachsthum des Herings im westlichen Theile der Ostsee. *Jahresbericht der Komm. z. wiss. Unters. der deutschen Meere in Kiel*, 4.–6. Jahrg., pp. 227–52.

MUŽINIĆ, S., 1931. Der Rhythmus der Nahrungsaufnahme beim Hering. *Ber. Deutsch. wiss. Komm. f. Meeresf.*, N.F., Bd. VI, pp. 62–4.

OGILVIE, H. S., 1934. A preliminary account of the food of the herring in the north-western North Sea. *Rapp. Proc.-Verb. Cons. Int. Explor. Mer.*, Vol. LXXXIX, Pt. 3, pp. 85–92.

ORTON, J. H., 1916. An account of the researches on races of herrings carried out by the Marine Biological Association at Plymouth 1914–15. *Journ. Mar. Biol. Assoc.*, Vol. XI, pp. 71–121.

EL SABY, M. K., 1932. The number of vertebrae in summer-spawning Manx herring. *40th Ann. Rep. Lancashire Sea-fish. Lab.*, pp. 139–48.

SAVAGE, R. E., 1937. The food of North Sea herring 1930–1934. *Min. Agric. Fish., Fish. Invest.*, Ser. II, Vol. XV, No. 5, pp. 1–60.

SCOTT, T., 1907. Some observations on the food of the herring. *25th Ann. Rep. Fish. Bd. Scotland* (1906), Pt. III, No. VI, pp. 260–71.

WAILES, G. H., 1936. Food of *Clupea pallasii* in southern British Columbia waters. *Journ. Biol. Board Canada*, Vol. I, pp. 477–86.

WILLIAMSON, H. C., 1914. A short résumé of the researches into the European races of herrings and the method of investigation. *Fisheries, Scotland, Sci. Invest.*, 1914, No. I, pp. 1–22.

WOOD, H., 1936. Race investigation of the herring population of Scottish waters. *Fisheries, Scotland, Sci. Invest.*, 1936, No. III, pp. 1–52.

—— 1937. Movements of herring in the northern North Sea. *Fisheries, Scotland, Sci. Invest.*, 1937, No. III, pp. 1–49.

THE SWIMMING AND BURROWING HABITS OF SOME SPECIES OF THE AMPHIPOD GENUS *BATHYPOREIA*

By E. Emrys Watkin, B.Sc., Ph.D.

Lecturer in Zoology, University College of Wales, Aberystwyth

(Text-figs. 1–2)

CONTENTS

	PAGE
Introduction	457
Swimming Habit	458
Burrowing Habit	461
Summary	465
References	465

INTRODUCTION

The amphipod family Haustoriidae is represented in the coastal waters of Great Britain by three genera, *Haustorius*, *Urothoë* and *Bathyporeia*, all three of which are characterized by the habit of burrowing into the soil of the sea floor. Dennell (1933) deals at some length with the swimming and burrowing habits of *Haustorius arenarius* in which he shows that (p. 387) "the animal swims on its back by the beating of the powerful pleopods...burrowing is a modification of the swimming movements, and is dependent on the expulsive action of the swimming current". Crawford (1937), referring to the burrowing Amphipoda of certain soils of the sea bottom near Plymouth, states (p. 638), "The local Haustoriidae burrow almost entirely by ejecting sand grains in a powerful swimming current", and in giving some details of the burrowing of *Urothoë brevicornis* and *U. grimaldii* var. *poseidonis* states that it is very similar to that of *Haustorius*. Schellenberg (1929), in dealing with the burrowing habits of some amphipods, gives an outline description of the process in *Bathyporeia robertsoni* Bate (probably *B. sarsi* Watkin, 1938). The author in this paper shows that the swimming and burrowing habits of four species of *Bathyporeia*, namely, *guilliamsoniana* (Bate), *elegans* Watkin, *pelagica* (Bate) and *pilosa* Lindström, are alike and similar to that of *B. robertsoni* as described by Schellenberg, but the process is described in much further detail. The burrowing habit differs considerably from that described by Dennell in *Haustorius*, in that it is dependent upon the sweeping action of the second gnathopods and first and second peraeopods aided by the first and second uropods; the swimming current takes no part in the process. The method of burrowing is more similar to that of *Ampelisca* which Crawford

(1937) states (p. 638) "is not dependent on a flow of water set up by the pleopods but is performed by the scraping and hauling of the gnathopods, aided by the urosome as soon as it gets a purchase".

SWIMMING HABIT

Movement has been observed in the four species *guilliamsoniana* (Bate), *elegans* Watkin, *pelagica* (Bate) and *pilosa* Lindström. No differences between the movement of the four species were observed. There are two types of movement, swimming and burrowing, which may follow each other in rapid succession. Swimming movements are effected by the pleopods. During this type of movement the body is held rigid and fully extended, the flagella of the antennules and antennae are laid back alongside the body, the pleon is fully extended which brings the first and second uropods close up beneath it, the third uropods depressed and in line with the pleon and converged in the median line (Fig. 2*a*). Thus a definite "stream-lining" effect is obtained.

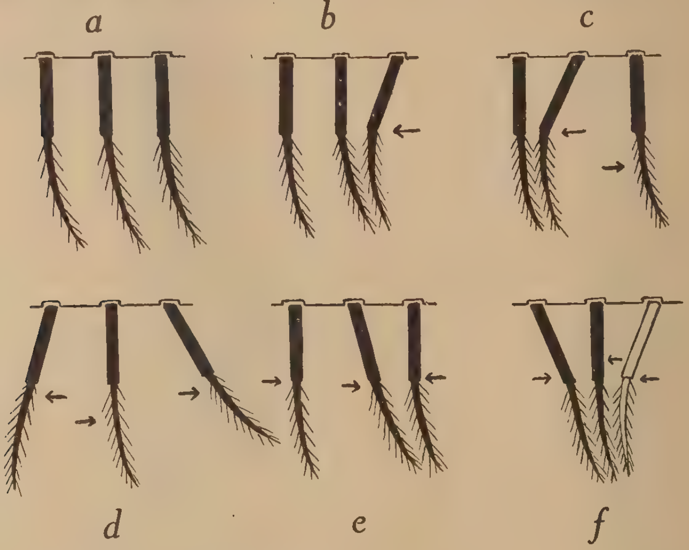


Fig. 1. Successive stages in the metachronal rhythm of the pleopods.

Pleopod movement is of the metachronal type. At rest the three pairs of pleopods are held hanging vertical to the pleon, and each pair is capable of a forward and backward movement from the rest position. Fig. 1*a* shows diagrammatically the rest position. Swimming commences with a forward movement of the third pair (*b*). The second pair now begin their forward movement and the third pair begin their backward movement and are now in the vertical position thus an inter-limb space is created between the second and third pairs and water flows in to fill this space (*c*). The first pair now commence their forward movement, the second pair have moved back to the vertical position, whilst the third pair are at the end of their backward stroke (*d*). Thus an inter-limb space is created between the first and second pairs and water flows in to fill this space. The first pair now begin the backward movement, the second pair have completed the backward stroke and the third pair are recovering to the rest position (*e*). Thus water is forced out between the second and third pairs. The completion of the beat is shown in (*f*) in which the first pair are at the end of their backward stroke, the second pair recovered to the rest position, whilst the third pair are moving forward for the next beat. Thus water is forced out from between the first and second pairs. Successive beats follow each other rapidly and the animal is driven forward through the water.

The rami of the pleopods are fringed with long feathered bristles (Fig. 2*g*). The bristles of the proximal end of the outer ramus are shorter and point outwards, those of the proximal end of the inner ramus are modified to serve as coupling hooks. The latter bristles have bifid tips with spear-shaped ends (g_2) and between the bifid tip the corresponding bristles of the opposite pleopod fit. The interlocking bristles can move freely within each other but cannot be withdrawn, due to the spear-shaped tips. The pleopods of a pair are further linked together by coupling hooks on the distal end of the basal joint (g_1). There are normally two coupling hooks on each basal joint, each with three recurved hooks into which the corresponding hooks of the opposite pleopod fit.

As a result of swimming movements currents of water are drawn in between the appendages and thus over the gills. The joints of some of the appendages are expanded and modified to form a ventral groove in which the gills are protected and in which in the female the brood pouch is formed. Anteriorly this groove is formed by the large coxal plates of the second peraeopods, the coxal plates of the second gnathopod and the first peraeopod lie alongside the mouthparts and are protective to them. Thus the ventral groove begins in the region of the second peraeon segment. The coxal plates of the third, fourth and fifth peraeopods are small and take no part in the formation of the ventral groove; their reduction is compensated by the expansion of some of the joints of these appendages. Peraeopod 3 is a doubly geniculate appendage, the basis is expanded and lies normally beneath its segment, the ischium is small and the large expanded merus is held at an angle of less than 90° to the basis and thus comes to lie partly at the side and partly posterior to it. The expanded basis of peraeopod 4 continues the side of the groove and it is completed by the basis of peraeopod 5 which is expanded on its posterior margin only. Thus the ventral groove is a feature of the peraeon only.

The first epimeral plate of the pleon is small; between it and the basis of peraeopod 5 is a space through which the water from the ventral groove passes out. The second and third epimeral plates are well developed, the

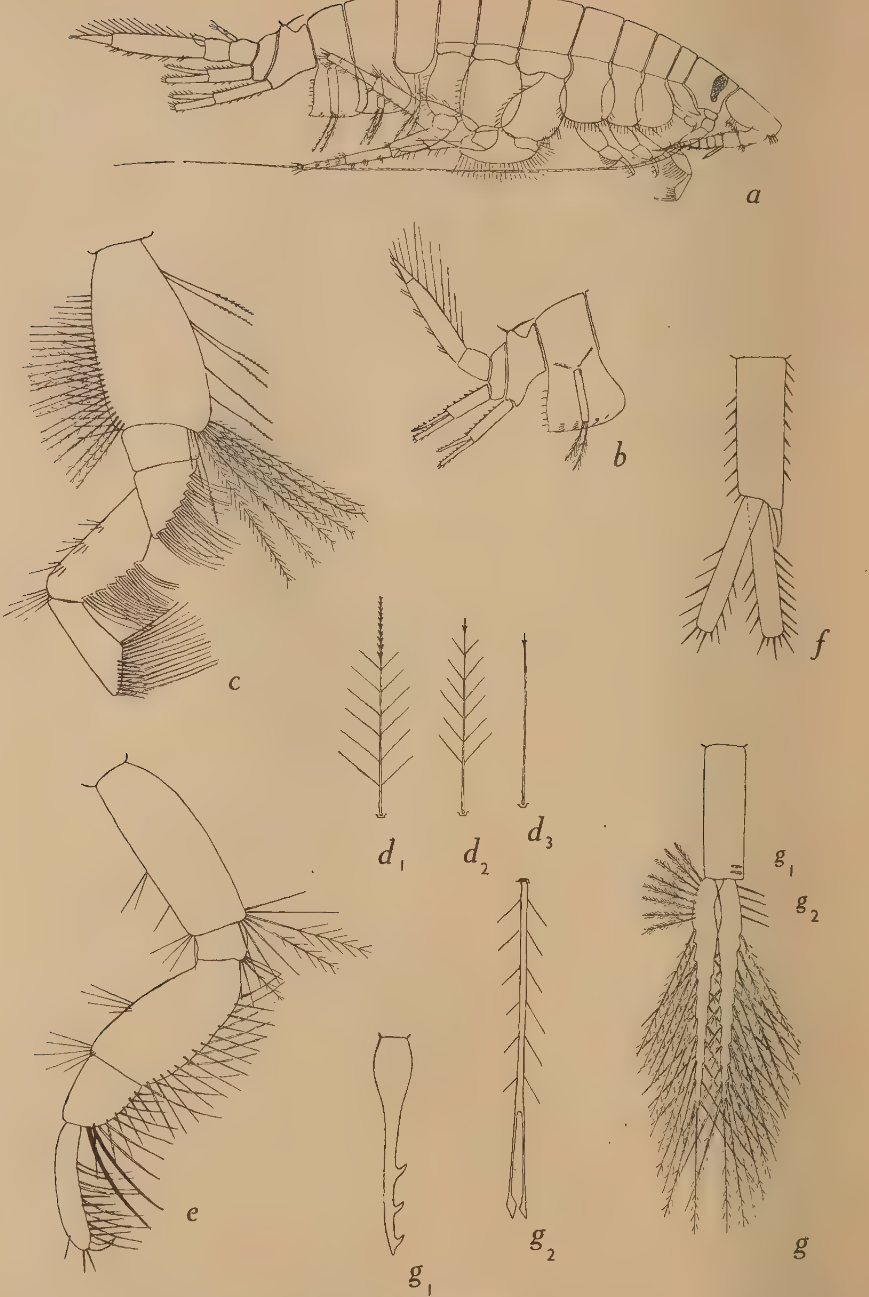


Fig. 2. Drawings based on *Bathyporeia guilliamsoniana* (Bate): *a*, animal in the swimming position; *b*, urosome in the burrowing position; *c*, second gnathopod; d_1, d_2, d_3, armature of bristles on anterior border of merus and carpus of the second gnathopod; *e*, first peraeopod; *f*, first uropod; *g*, pleopod; g_1, coupling hook on basal joint; g_2, modified feathered bristle from base of inner margin of inner ramus.

second is convex anteriorly and concave posteriorly, the third typically rounded at both ends. Between the epimeral plates the pleopods work in unison to draw water through the ventral groove, and the urosome bends forward to push sand particles backwards beyond the animal.

Two main water currents are drawn into the ventral groove. The main current enters anteriorly between the second gnathopods. This current passes in well beneath the mouthparts; there is no evidence that any part of it is deflected on to the mouthparts and thus no evidence of feeding on small particles held in suspension in the water current. The entrance to the ventral groove is guarded by a series of long heavily feathered bristles which arise from the distal end of the basis of the second gnathopod; they form an effective filter for the larger particles suspended in the water current. A subsidiary water current is drawn in between the anteriorly directed second peraeopod and the backwardly directed third peraeopod. This opening is guarded by an extensive development of feathered bristles along the anterior margin of the basis, ischium and merus of peraeopod 3, and the water current is thus filtered of the larger particles in suspension. The feathered bristles are directed inwards, and although those of the opposite sides do not meet they form an effective filter for practically all the water that enters at this point.

BURROWING HABIT

The second type of movement is that of burrowing into the sand which is the natural home of the species in this genus. Evidence is now available to show that the various species feed by cleaning sand particles and that swimming is a diversion probably connected mainly with reproduction when the tide covers them. They thus resemble in their habits certain cumaceans (Foxon, 1936) which live in the same type of habitat, and in some localities, e.g. Kames Bay, Millport, may be found in the same samples.

It has been shown that in the swimming movement the body is held rigid and fully extended with the pleon in line with the rest of the body, the first and second uropods laid back beneath the urosome, the third uropods extended and in line with the pleon and with their right and left rami converged to the middle line. The rami can be easily diverged from each other and it is suggested, although proof is difficult to obtain, that they may act as steering organs. The swimming movement eventually carries the animal head first into the sand when swimming ceases and burrowing begins. Penetration of the sand is assisted by the form of the antennule. The basal joint is large and extends forward in direct line with the head, with its proximal end broad and narrowing to the distal end, which thus is spear-shaped when viewed from above and acts as a ploughshare to penetrate the sand. The distal end of this basal joint carries a group of spines which point outwards in the direction in which the animal enters the sand. The second joint arises from the underside of the basal joint, and the whole limb beyond the basal joint can be laid back alongside the body. Similarly, the antenna can be laid back alongside the body, so that the anterior end of the body is triangular when viewed from the side and above, making rapid penetration of the sand an easier matter. The force of the swimming movement is sufficient to carry the head end into the sand and thus to bring the sand within reach of the burrowing appendages, which are the second gnathopods and first and second peraeopods. These three pairs of appendages are so arranged that the second gnathopods lie parallel with each other in the median plane; the first peraeopods diverge somewhat and come to lie outside and somewhat posterior to the second gnathopods; the second peraeopods also diverge and come to lie outside and somewhat posterior to the first peraeopods. The first gnathopods are small and are used as feeding appendages and are intimately associated with the mouth-parts; thus the area beneath the head is free for the action of the burrowing limbs, which are flexed at the ischium and can be projected forward and drawn back with rapidity. The second gnathopods can extend forward to beneath the antennules; they sweep the sand particles backwards to within reach of the first and second peraeopods, which sweep the sand backwards towards the posterior end of the animal where it comes within reach of the first and second uropods. The three anterior burrowing limbs do not work in unison, the second gnathopod has a more rapid action than the peraeopods, all three, however, take a deep backward sweep before being drawn upwards and pushed forward for the next sweep.

Associated with the second gnathopods and first and second peraeopods in the burrowing movement are the first and second uropods. They, by means of flexion and extension of the pleon, sweep sand particles backwards beyond the animal. The pleon is flexed between the third and fourth segment. As a result of the flexion of the pleon the first and second uropods are carried forward, but the more delicate third uropods are raised into a vertical plane and are thus removed from the sphere of action of the first and second uropods (Fig. 1 *b*). The outer rami only of the third uropods are well developed and their inner margin is fringed with an edge row of long feathered bristles. The rami can be diverged from each other, and when held in the vertical position on the flexion of the pleon they are always widely separated. They thus act as a brake on the rapidity of the forward movement.

It is instructive to observe the animal attempting to burrow in very shallow sand in a dish, thus imitating and prolonging the first movements in the burrowing process. The abdomen is held in extension and sand particles are shot backwards beyond the animal from the second gnathopods and first and second peraeopods, being caught in the water issuing in the swimming movement from the ventral groove. This movement continues until full swimming in the water recommences. When the animal enters sand sufficiently deep to cover the body the first sweeps of the anterior burrowing appendages cause the sand particles to be flung back in the same way, but as the weight of sand to be moved becomes greater the rate of movement is reduced, the pleon is flexed, the first and second uropods come into service and the third uropods are raised, further reducing the speed of forward movement which now becomes a crawl through the sand. When the animal is placed on dry sand no attempt is made to burrow, but when the sand is damped but not covered with water penetration can be effected. On substituting mud for the sand no attempt is made to burrow, the animal swims round spasmodically and mud particles accumulate on the appendages.

The first and second uropods are robust appendages with the two rami of about equal length with no linking apparatus between the basal joints of a pair. The rami usually converge, but in the backward sweep, i.e. pleon extension, they diverge and thus cover a greater area, the arrangement of spines on their margins closing the gap between them. On the flexion of the pleon they converge and can thus be drawn back freely. The first uropods are longer than the second pair and work to the outside of them, thus sweeping sand away from underneath the whole width of the pleon.

The function of the third, fourth and fifth peraeopods in the burrowing process is somewhat doubtful, although some of their functions seem clearly indicated. It has already been shown that the basis of the three limbs and the merus of peraeopod 3 take part in the formation of the ventral groove. The merus of peraeopod 3 is fringed on its outer face near the anterior border with a row of spines which project outwards at right angles to the face of the joint. Their function is to prevent sand particles falling from above on to the edge row of feathered bristles of the merus which filters the water current entering at this point. The carpus and propodus of peraeopod 3 are reduced, geniculate to the merus and held alongside the body outside the expanded basis of peraeopod 4. The outer edge of the propodus carries a row of spines held at right angles to the outer face of the joint, and thus they also prevent sand particles from falling from above. The basis of peraeopod 4 is held normally beneath its segment, but from the ischium the limb is flexed to be held alongside the body outside peraeopod 5 and pointing dorsally and posteriorly, and diverging outwards. It is capable of a slight up-and-down and back-and-fore movement. Its main function seems to be the prevention of sand particles from falling from above; the inner face of the joint carries a group of spines and bristles which extend across the space between it and the body. It may assist burrowing by a forward push against the sand particles. Peraeopod 5 is also flexed at the ischium and is held pointing downwards and backwards. In its armature it carries a less number of bristles but a greater number of spines. This appendage from its position cannot prevent sand particles from falling from above; it may prevent sand particles falling inwards from the sides or possibly help to push the animal forward through the sand.

A detailed description of the second gnathopod, first and second peraeopods and first and second uropods will assist an understanding of the way in which these appendages are modified to serve the burrowing process.

Second gnathopod (Fig. 2*c*). The basis is rectangular in outline; the anterior edge carries a row of simple bristles, the outer face a row of heavily feathered bristles, the inner face a row of serrated bristles, the posterior edge a few long serrated bristles. The distal edge of this joint carries a row of long feathered bristles, which together with those of the opposite limb form an effective filter to prevent large particles entering the ventral groove along with the main water current which enters through them. The ischium is small and square with a tuft of feathered bristles and simple bristles on its distal posterior edge; the feathered bristles assist in filtering the water current. The merus, carpus and propodus project forwards. The merus is triangular with up to seven groups of bristles on its posterior margin, each group is horseshoe-shaped, the end bristles of each group are simple bristles (d_3), the centre ones serrated feathered bristles (d_1) with feathered bristles in between (d_2). The carpus has a curved posterior edge which carries up to seven groups of bristles as on the merus. The anterior edge of the carpus carries about four groups of simple bristles. The propodus is spatulate with the ventral surface deeply grooved; the edges of the groove carry a row of well-developed spines which are fundamentally arranged on the same horseshoe-shaped pattern as on the merus and carpus, but the rows are broken by the hollow ventral surface. On the outer edge at the distal end is a row of about twelve stout spines. The bristles on the merus, carpus and propodus are curved backwards to assist in the process of sweeping the sand particles. The dactylus is absent.

The *first peraeopod* (Fig. 2*e*) is stoutly built with the basis rectangular with a few serrated bristles and ordinary bristles on the anterior margin near the base and with a few feathered bristles and ordinary bristles near the apex. The feathered bristles assist in filtering the water current entering the ventral groove. The ischium is small and square. The merus and carpus are broad with an inner face row and outer face row of simple bristles on the anterior margin. The distal end of the anterior margin of the carpus bears a pair of much stronger spines with two other spines not so well developed. These strong spines are somewhat hooked and are the main sweeping structures on this appendage. The merus and carpus are somewhat geniculate to the ischium. The propodus is smaller, not swollen, with the anterior edge carrying a row of spines and the outer and inner faces with a row of bristles. The dactylus is claw-like. The inner and outer face rows of bristles on the merus, carpus and propodus extend laterally to aid the sweeping movement. The absence of heavily feathered bristles show this appendage to be mainly sweeping in function and not assisting to any extent in filtering the water current entering the ventral groove.

The *second peraeopod* is built on the same plan as the first with the same armature; the only comment necessary is that the spines of the edge row on the propodus are stronger.

The *first* and *second uropods* (Fig. 2*f*) are stoutly built with the basal joint carrying a row of small spines on outer and inner edges. The distal end of the outer edge carries a stout spine. The inner and outer rami are of equal length and the inner arises immediately dorsal to the outer. The inner and outer rami carry a row of stout spines along their inner and outer edges and around the apex. The ventral surface carries a few scattered bristles.

This work was in part carried out at the Laboratory of the Scottish Marine Biological Association, Millport. My thanks are due to the Director, Mr Richard Elmhirst, for the facilities afforded me there.

Summary

The swimming and burrowing habits of four species of the genus *Bathyporeia* have been examined and shown to be alike, and similar to *B. robertsoni* as described by Schellenberg.

Swimming is effected by the pleopods working in a metachronal rhythm, drawing water along a ventral groove formed by the coxal plates of the second peraeopods and the expanded bases of peraeopods 3, 4 and 5.

The main water current enters anteriorly between the second gnathopods and is filtered by a series of feathered bristles borne on the basis of this appendage; a subsidiary current enters between the second and third peraeopods.

Burrowing is effected mainly by the sweeping action of the second gnathopods and first two pairs of peraeopods, aided by the first and second uropods as soon as they can obtain a purchase on the sand. The adaptation of these three pairs of appendages to burrowing is explained.

The method of burrowing is different from that described by Dennell for *Haustorius* and appears to be more nearly related to that of *Ampelisca*.

REFERENCES

Crawford, G. I., 1937. Notes on the distribution of burrowing Isopoda and Amphipoda in various soils on the sea bottom near Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xxi, p. 638.

Dennell, R., 1933. The habits and feeding mechanism of the amphipod *Haustorius arenarius* Slabber. *Journ. Linn. Soc. Zool. London*, Vol. xxxviii, p. 387.

Foxon, G. E. H., 1936. Notes on the natural history of certain sand-dwelling Cumacea. *Ann. Mag. Nat. Hist.*, Ser. 10, Vol. xvii, pp. 377–393.

Schellenberg, A., 1929. Körperbau und Grabweise einiger Amphipoden. *Zool. Anz. Leipzig*, Vol. lxxxv, pp. 186–190.

Watkin, E. E., 1938. A revision of the amphipod genus *Bathyporeia* Lindström. *Journ. Mar. Biol. Assoc.*, Vol. xxiii, pp. 211–236.

THE PELAGIC PHASE IN THE LIFE HISTORY OF THE AMPHIPOD GENUS *BATHYPOREIA*

By E. Emrys Watkin, B.Sc., Ph.D.

From the Department of Zoology, University College of Wales,
Aberystwyth, and the Marine Biological Station, Millport

(Text-figs. 1–2)

CONTENTS

	PAGE
Introduction	467
The *Bathyporeia* fauna of the sand of Kames Bay	468
Analysis of the tow-net samples	471
Relationship to lunar month	475
Discussion	475
Summary	480
References	480

INTRODUCTION

During the year 1936 Mr Richard Elmhirst, Director of the Scottish Marine Biological Station at Millport, carried out a series of tow-nettings across the waters of Kames Bay at varying times after nightfall, mainly between the hours of 10 p.m. and midnight, to ascertain the nature and extent of the faunal immigration into the bay from outside waters, and of the nocturnal and vertical movement of the fauna which normally lies buried in the sand during the day. The net employed was an ordinary coarse tow-net supplemented on occasions with a finer net; however, the latter net captured but few amphipods and its results will be neglected in the present paper. The method employed was to walk into the water at the edge of the incoming or outgoing tide to a depth of about 2 ft. and to walk across the bay following the edge of the tide trailing the net about 10 ft. posteriorly and at arms' length into the tidal flow, thus avoiding as far as possible disturbances set up in the water by the walking movement. Each sample consisted of a tow of approximately 100 yards. Thus the position of each sample is determined by the time it was taken in relation to the day of the lunar month, and samples were obtained at all levels from high-water mark to low-water mark. I am indebted to Mr Elmhirst for the opportunity of examining the *Bathyporeia* taken in these samples and for his critical comments during this investigation.

THE *BATHYPOREIA* FAUNA OF THE SAND OF KAMES BAY*

An appreciation of the nocturnal vertical movement of these amphipods into the water of the tidal flow necessitates an analysis of their abundance in the intertidal sand. During the latter half of March 1937 a series of three traverses were sampled from the high-water mark of spring tides to the low-water mark of spring tides. Each traverse was sampled at intervals of approximately 5 yards. Each sample consisted of the fauna obtained by sieving the sand from a surface area of one square foot, to a depth of 1 in., through a brass wire sieve of 30 meshes to the linear inch. Experience on Kames Bay and elsewhere had shown that these amphipods do not bury themselves deeply into the sand and that the total population, apart from the newly hatched forms, which can pass through the meshes of the sieve, may be captured by this means.

The first traverse was taken approximately along the centre line of the bay and the second and third respectively at a distance of 20 yards to the left and right of the first. The result of the analysis of the samples is given in Table I and is represented diagrammatically against the background of the bay in Fig. 1.

Four species of the genus *Bathyporeia* occur in this area (Watkin, 1938), *B. pilosa* Lindström, *B. pelagica* Bate, *B. elegans* Watkin, and *B. guilliamsoniana* Bate, and they show a definite zonation from high-tide mark to low-tide mark. The upper 30 yards of the 200 yard traverse show a complete absence of *Bathyporeia*. The next 45 yards is occupied by *B. pilosa*, which forms a definite belt across the bay sharply demarcated at its upper and lower limits, particularly the latter. The concentration of individuals in the centre of this belt is particularly heavy; as many as 1205 individuals per square foot are recorded, with an average number per sample of almost 300. The sharpness of the lower edge of the belt is particularly noteworthy; thus sample 12 in traverse three gave 1205 individuals whilst 5 yards nearer low-water mark the number drops to 42 and the next sample records the lower limit of the belt. There follows an area of 35 yards, samples 16–22, barren of *Bathyporeia*, with *B. pelagica* appearing in sample 23 and forming a second well-defined belt across the bay 40 yards in width, disappearing in sample 31. The concentration of *B. pelagica* is very considerably less than that of *B. pilosa*, averaging less than 20 per square foot. The third zone is formed by *B. elegans* which overlaps to some extent the *B. pelagica* zone and continues to the

---

* Kames Bay, Great Cumbrae, is a comparatively small bay bounded on the north-land side by the Marine Promenade of Millport and on the east and west side by sandstone rocks which wear down to a fine reddish sand unmixed with clay which forms the soil of the bay. On the south side the bay is open to the waters of the Firth of Clyde, the island of Little Cumbrae and the two promontories which form the southern points of the island of Great Cumbrae afford some protection. At low tide a stretch of sand roughly 280 yards from east to west and 180 yards from north to south is exposed.

TABLE I. NUMBER OF INDIVIDUALS OF *BATHYPOREIA* PER SQUARE FOOT IN TRAVERSES I, II AND III

Sample numbers in each traverse are at corresponding tide levels
A, *B. pilosa*; B, *B. pelagica*; C, *B. elegans*; D, *B. guilliamsoniana*

Sample no.	Traverse I				Traverse II			
	A	B	C	D	A	B	C	D
1–6	None				None			
7	..	..	..	..	8	..	..	..
8	6	..	..	..	110	..	..	..
9	428	..	..	..	106	..	..	..
10	166	..	..	..	361	..	..	..
11	708	..	..	..	507	..	..	..
12	39	..	..	..	923	..	..	..
13	8	..	..	..	6	..	..	..
14	7	..	..	..	5	..	..	..
15	4	..	..	..	..	..	..	..
16–22	None				None			
23	..	..	..	..	..	2	..	..
24	..	1	..	..	..	18	..	..
25	..	8	..	..	..	31	..	..
26	..	9	..	..	..	126	..	..
27	..	7	..	..	..	37	..	..
28	..	1	..	..	..	5	..	..
29	..	3	..	..	..	3	..	..
30	..	7	11	1	..	..	10	1
31	..	1	4	..	..	..	18	..
32	..	..	16	..	..	..	41	5
33	..	..	26	5	..	..	35	..
34	..	..	37	5	..	..	39	1
35	..	..	47	5	..	..	29	4
36	..	..	37	4	..	..	..	..

Sample no.	Traverse III				Average for three traverses			
	A	B	C	D	A	B	C	D
1–6	None				None			
7	95	..	..	..	34	..	..	..
8	357	..	..	..	158	..	..	..
9	483	..	..	..	339	..	..	..
10	860	..	..	..	462	..	..	..
11	788	..	..	..	668	..	..	..
12	1205	..	..	..	722	..	..	..
13	42	..	..	..	19	..	..	..
14	..	..	..	..	4	..	..	..
15	..	..	..	..	1	..	..	..
16–22	None				None			
23	..	4	..	..	..	2	..	..
24	..	6	..	..	..	8	..	..
25	..	17	2	..	..	19	1	..
26	..	47	..	..	..	61	..	..
27	..	99	2	..	..	48	1	..
28	..	29	6	..	..	12	2	..
29	..	21	12	1	..	9	4	..
30	..	10	21	7	..	6	14	3
31	..	1	14	..	..	1	12	..
32	..	..	22	..	..	..	26	2
33	..	..	39	5	..	..	33	3
34	..	..	38	10	..	..	38	5
35	..	..	27	1	..	..	34	3
36	..	..	..	..	..	..	12	1

low-water mark of spring tides; sampling beyond low-water mark shows its presence to some depth. Its heaviest concentration is near low-water mark and its abundance is somewhat less than that of *B. pelagica*. The fourth species, *B. guilliamsoniana*, occurs but spasmodically amongst the *B. elegans*, but it becomes abundant and dominant beyond low-water mark.

All the individuals of *pelagica*, *elegans* and *guilliamsoniana*, and a sample of *pilosa*, from the first traverse, were examined to ascertain the proportion of males to females, and of adult forms to immature forms. Adult maleness was determined by examination of the antenna, adult femaleness by either the presence of eggs in the brood pouch, by setose oostegites, or by the antennae. Individuals are listed as immature if the secondary sexual characters have begun their development, young if the secondary sexual characters are not shown. The result of this analysis is shown in Table II.

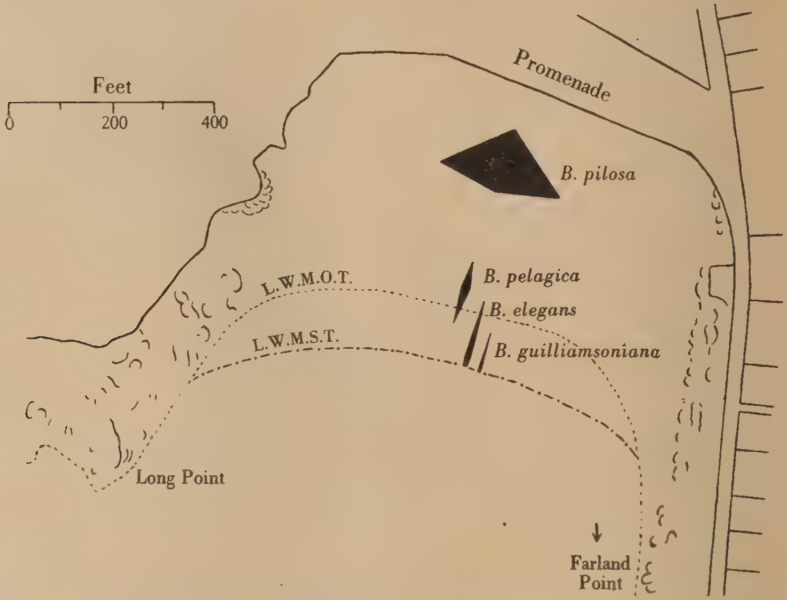


Fig. 1. Zonation of *Bathyporeia* in Kames Bay. Horizontal scale = 1000 individuals to 1 in.

Thus, neglecting the differences between the species, the adult male population represents about 15%, the adult female population about 26%, giving a ratio of adults to immature and young forms of 41 to 59. It must be borne in mind that the sampling took place in March, when it may be expected that the proportion of adult forms would be at its peak after the almost complete winter cessation of reproduction and before many, if any, of the new season's population are released from the brood pouch. The above figures show a small percentage only of young forms; this percentage is probably too low since some young forms, if present, may have escaped through the meshes of the sieve. However, from the point of view of subsequent discussion the main points to be noted are the small percentage of adult males and the much larger percentage of adult females.

TABLE II. ANALYSIS OF THE SEX AND AGE OF THE SPECIES

	Adult ♂	Adult ♀	Immature ♂	Immature ♀	Young forms	Total
B. pilosa	175	260	264	176	14	889
B. pelagica	5	32	66	63	56	222
B. elegans	13	36	13	43	67	172
B. guilliamsoniana	2	3	3	1	2	11
Total	195	331	346	283	139	1294

ANALYSIS OF THE TOW-NET SAMPLES

Table III gives the date, time of day when the sample was taken, age of the moon in days, time of high water and species content of forty-six samples taken during the year 1936. One sample only, that of September 30, did not contain any *Bathyporeia*. Thus it may be assumed that some vertical migration into the tidal waters takes place on almost every night of the year. Other samples taken at various times in previous years confirm this view. However, the number per sample is very variable. Of the forty-five samples containing these amphipods twenty gave less than ten individuals, seventeen samples from ten to fifty individuals, four samples from fifty to 100 individuals, four samples from 100 to 200 individuals and one only over 300 individuals. In view of the high concentration in the sand larger numbers might have been expected in the samples.

The total numbers for each species show a direct relationship to the numbers in the sand with *pilosa* as the dominant form, with *pelagica* and *elegans* in considerably less numbers and with an occasional *guilliamsoniana*. The individual samples show that, in the main, each species retains its purity when migrating into the tidal waters. Thus thirty-two of the forty-five samples show one species only, eight a mixture of two species, four a mixture of three species, and one only with the four species. It may be expected that *pilosa*, since it occupies a definite zone on the beach away from the other species, would retain its purity. This is so, in that twenty-two of the samples contain this species only and where it does occur in a mixed species sample its numbers are few. On the other hand, the *pelagica* and *elegans* belts overlap to some extent and some admixture of the two species in the tidal waters may be expected. However, here again the samples containing these species are remarkably pure, and where a mixture of more than one species occurs the sample is dominated by one of the species.

It is noteworthy that the species retain their zonation so closely when swimming in the tidal waters, which suggests that the time they remain in the water is short. Possibly they make several short excursions from the sand,

TABLE III. NUMBER OF INDIVIDUALS OF EACH SPECIES PER SAMPLE

A, *B. pilosa*; B, *B. pelagica*; C, *B. elegans*; D, *B. guilliamsoniana*

Date	Age of moon in days	G.M.T.	Time of H.W. p.m. G.M.T.	A	B	C	D	Total
7. i. 36	14	10.00 p.m.	11·44	23	..	..	..	23
15. i. 36	22	7.30 p.m.	4.16	..	8	..	..	8
21. i. 36	28	10.30 p.m.	10.32	1	..	..	..	1
12. ii. 36	20	8.30 p.m.	3·7	..	..	1	..	1
13. ii. 36	21	7.00 p.m.	3·37	..	4	..	..	4
4. iii. 36	12	11.00 p.m.	10.38	21	..	..	..	21
19. iii. 36	27	9.00 p.m.	9.34	152	..	..	..	152
24. iii. 36	2	4.30 p.m.	1·0	56	..	1	..	57
29. iv. 36	9	10.15 p.m.	6.53	..	16	2	..	18
30. iv. 36	10	10.15 p.m.	8.10	11	..	..	1	12
1. v. 36	11	10.15 p.m.	9.13	3	..	..	..	3
2. v. 36	12	10.15 p.m.	10.2	32	..	..	..	32
3. v. 36	13	10.15 p.m.	10.44	69	..	..	..	69
9. v. 36	19	10.15 p.m.	1.55	2	6	8	1	17
14. v. 36	24	10.15 p.m.	5.55	145	..	..	..	145
15. v. 36	25	10.15 p.m.	7.9	1	37	2	..	40
16. v. 36	26	10.15 p.m.	8.17	4	8	..	1	13
17. v. 36	27	10.15 p.m.	9.19	5	5	..	..	10
21. v. 36	2	10.15 p.m.	0.22	24	..	..	..	24
1. vi. 36	13	10.15 p.m.	10.0	37	..	..	..	37
10. vi. 36	22	11.00 p.m.	3.49	5	3	1	..	9
12. vi. 36	24	10.30 p.m.	5.32	..	..	1	..	1
16. vi. 36	28	10.30 p.m.	9.52	37	..	..	..	37
23. vi. 36	5	1.00 a.m.	3.12	143	1	..	..	144
26. vi. 36	8	11.00 p.m.	5.12	..	1	5	..	6
27. vi. 36	9	1.00 a.m.	5.58	..	..	7	..	7
2. vii. 36	14	11.00 p.m.	10.53	14	..	..	..	14
14. vii. 36	26	11.00 p.m.	8.23	..	11	..	..	11
21. vii. 36	4	11.00 p.m.	2.9	..	8	..	..	8
31. vii. 36	14	11.00 p.m.	10.30	370	..	..	..	370
12. viii. 36	26	11.00 p.m.	8.11	2	71	..	..	73
21. viii. 36	5	11.00 p.m.	2.41	..	2	..	..	2
31. viii. 36	15	11.00 p.m.	11.35	1	..	..	..	1
8. ix. 36	23	9.45 p.m.	5.11	..	4	81	1	86
15. ix. 36	1	10.00 p.m.	0.6	32	..	..	..	32
24. ix. 36	10	10.00 p.m.	5.28	1	12	..	..	13
30. ix. 36	16	10.00 p.m.	11.50	..	..	..	..	..
5. x. 36	21	10.30 p.m.	3.9	..	..	4	..	4
20. x. 36	6	10.30 p.m.	2.41	..	3	..	..	3
28. x. 36	14	10.30 p.m.	10.38	1	..	..	..	1
7. xi. 36	24	8.30 p.m.	7.0	2	..	..	..	2
12. xi. 36	29	10.30 p.m.	11.24	1	..	..	..	1
25. xi. 36	12	8.30 p.m.	9.14	3	..	..	..	3
11. xii. 36	28	11.30 p.m.	10.58	6	..	..	..	6
14. xii. 36	2	8.45 p.m.	0.25	26	..	..	..	26
22. xii. 36	10	7.30 p.m.	6.19	4	..	..	..	4
			Total	1234	200	113	4	1551

which may account to some extent for their scarcity, compared with the numbers in the sand and also their ability to remain within the orbit of their belt in the sand. Their behaviour in a dish in the laboratory, although under totally different environmental conditions, confirms this, for an individual will emerge from the sand, swim around the dish for a short time and return to the sand. It cannot be imagined that they perform extensive migrations during the intertidal period and yet return to their particular zone area with the retreating tide. This zonation is further shown when the time of sampling is related to the time of high water. The high-tide samples are composed of *pilosa*, the mid-tide samples of *pelagica*, and the low-tide samples of *elegans*. When the samples are related to whether they were taken on a falling tide or a rising tide little of value emerges. In general the average number per sample is greater when taken on a falling tide. This point requires further investigation.

An analysis of the individuals of each species into their sexual age, for the population obtained by the tow-net, is given in Table IV.

The immediate noticeable feature is the preponderance of adults over immature forms as compared with the numbers shown in Table II for the sand population. The total figures for all species combined give an adult population of over 57% as compared with 40%. Of the 57% of adults, 42% are adult males and 15% adult females. Thus the dominance of adult males in the tow-net samples is a marked one.

Considering the species individually, of 1234 individuals of *pilosa* taken in the tow-net samples 57% are adults (40% males and 17% females), 31% are immature and 12% young forms. This dominance of adults is actually much more marked than the actual figures suggest since of the 148 young forms, 123 were obtained in two samples, those of June 23 and July 31. A study of the individual samples shows a considerable variation. An occasional sample like that of March 24 is composed almost entirely of adult males; no sample shows a dominance of adult females. Other samples are composed almost entirely of a mixture of adult males and females, such as that of May 14, whilst others show a high percentage of immature and young forms.

A similar variable population occurs in *pelagica* with 70% adult (60% male and 10% female), with 18% of immature forms and 12% of young forms. As in *pilosa* some samples are almost completely composed of adult males, others with a mixed population of adult males and females, and others with a considerable percentage of young forms.

The figures for *elegans* show the same general outline as in the above two species with a marked dominance of adult males. Only four individuals of *guilliamsoniana* were taken and of these three were adult males.

TABLE IV. NUMBER OF INDIVIDUALS IN EACH SAMPLE AT EACH MATURITY STAGE

A = adult males, B = adult females, C = immature males with secondary sexual characters developing, D = immature females with secondary sexual characters developing, E = young males and females with no secondary sexual characters showing.

Date	A	B	C	D	E	Total
			B. pilosa			
7. i. 36	4	..	12	3	4	23
21. i. 36	..	..	..	1	..	1
4. iii. 36	13	6	2	..	..	21
19. iii. 36	76	21	34	19	2	152
24. iii. 36	52	1	2	1	..	56
30. iv. 36	9	..	2	..	..	11
1. v. 36	2	..	..	1	..	3
2. v. 36	22	7	1	2	..	32
3. v. 36	59	6	2	2	..	69
9. v. 36	2	..	..	..	..	2
14. v. 36	98	37	10	..	..	145
15. v. 36	1	..	..	..	..	1
16. v. 36	3	1	..	..	..	4
17. v. 36	2	..	3	..	..	5
21. v. 36	14	8	..	..	2	24
1. vi. 36	27	3	2	..	5	37
10. vi. 36	3	..	1	..	1	5
16. vi. 36	2	12	6	9	8	37
23. vi. 36	64	12	13	3	51	143
2. vii. 36	5	6	2	1	..	14
31. vii. 36	16	69	81	131	73	370
12. viii. 36	2	..	..	..	..	2
31. viii. 36	1	..	..	..	..	1
15. ix. 36	12	7	4	7	2	32
24. ix. 36	..	..	1	..	..	1
28. x. 36	..	..	..	1	..	1
7. xi. 36	1	..	1	..	..	2
12. xi. 36	..	..	..	1	..	1
25. xi. 36	1	..	1	1	..	3
11. xii. 36	1	1	4	..	..	6
14. xii. 36	3	6	11	6	..	26
22. xii. 36	..	..	3	1	..	4
Total	495	203	198	190	148	1234
			B. pelagica			
15. i. 36	2	1	3	2	..	8
13. ii. 36	2	..	..	1	1	4
29. iv. 36	13	3	..	..	..	16
9. v. 36	4	..	..	2	..	6
15. v. 36	35	1	1	..	..	37
16. v. 36	4	1	1	2	..	8
17. v. 36	3	2	..	..	..	5
10. vi. 36	2	1	..	..	..	3
23. vi. 36	1	..	..	..	..	1
26. vi. 36	1	..	..	..	..	1
14. vii. 36	5	..	3	3	..	11
21. vii. 36	5	2	1	..	..	8
12. viii. 36	31	4	6	7	23	71
21. viii. 36	1	..	..	1	..	2
8. ix. 36	2	..	1	1	..	4
24. ix. 36	8	3	1	..	..	12
20. x. 36	1	2	..	..	..	3
Total	120	20	17	19	24	200

TABLE IV (CONTINUED).

Date	A	B	C	D	E	Total
B. elegans						
12. ii. 36	1	..	..	..	..	1
24. iii. 36	..	..	1	..	..	1
29. iv. 36	2	..	..	..	..	2
9. v. 36	8	..	..	..	..	8
15. v. 36	2	..	..	..	..	2
10. vi. 36	1	..	..	..	..	1
12. vi. 36	1	..	..	..	..	1
26. vi. 36	1	..	1	..	3	5
27. vi. 36	3	..	..	..	4	7
8. ix. 36	9	18	27	18	9	81
5. x. 36	2	..	1	1	..	4
Total	30	18	30	19	16	113
B. guilliamsoniana						
30. iv. 36	1	..	..	..	..	1
9. v. 36	1	..	..	..	..	1
16. v. 36	1	..	..	..	..	1
8. ix. 36	..	..	..	1	..	1
Total	3	..	..	1	..	4

RELATIONSHIP TO LUNAR MONTH

The age of the moon in days (with day 1 as the first day of the new moon) is given in the second column in Table III. If Table IV be rearranged according to the day of the lunar month and all species be considered together irrespective of the season of the year, an indication of the relationship of the occurrence of *Bathyporeia* with the lunar month can be obtained. These results are represented graphically in Fig. 2.

The result is somewhat uneven, but in general it may be concluded that the number of individuals appearing in the tidal waters increases to two maxima which correspond to the periods immediately preceding full moon and preceding and partly overlapping the appearance of the new moon. The period immediately following the full moon is marked by a distinct scarcity of individuals, although this period is rather inadequately covered by the sampling. A second period of scarcity occurs at the end of the first quarter and beginning of the second quarter. A more detailed study shows that there is no difference in the nature of the population at the two maxima; both are represented by the same proportion of males to females and of adults to young forms. In the figure all four species are grouped together, an attempt to show variability in the behaviour of *pilosa*, *elegans* and *pelagica* gave negative results and detailed figures have consequently been omitted.

DISCUSSION

The vertical movement of amphipods whose habitat is normally in the soil of the sea floor is a phenomenon which has been recorded by many authors. It is, however, necessary to distinguish between species whose vertical movements are mainly confined to the hours of daylight and those in which such movement occurs only during the hours of darkness. It is with the latter only that this paper is mainly concerned, and reference to three main papers may be made, Tattersall (1913*a*), Elmhirst (1932), and Fage (1933). Tattersall in his survey of the amphipods of Clare Island and the adjoining district states that "tow-netting in the harbours and shallow waters...at the surface at night has yielded excellent results", and of eighty-four species of gammarid amphipods recorded eleven are given as occurring in plankton samples taken during the night and twelve as taken in plankton samples during the daytime. Only one species, *Guernea coalita* (Norman), is recorded as occurring in both the day and night hauls. He gives no details of the sex or age of the specimens captured, but informs me that they were predominantly adult males. Tattersall in another paper (1913*b*) shows that many mysids and cumaceans become abundant in the surface waters at night time. Elmhirst records the night tidal migrants of Kames Bay and shows that *Gammarus locusta*, *Bathyporeia* sp., *Pontocrates* sp., *Megalopurus agilis*, *Periculodes longimanus* and *Paratylus swammerdami* are common forms in the night population of the waters of this bay, together with the mysid *Schistomysis spiritus* and the cumacean *Pseudocuma cercaria*. Some details of the age and sex are given. Fage in an

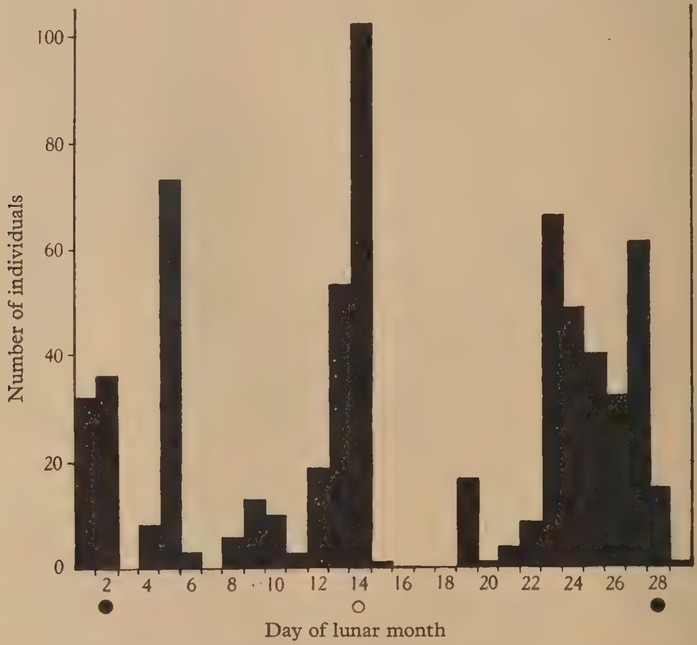


Fig. 2. Average number of individuals per day of lunar month.

extensive series of samples taken at Banyuls-sur-Mer and at Concarneau at night time, "autour d'un foyer lumineux", records thirty-four species of gammarid amphipods together with several mysids and cumaceans. Comparing the lists of amphipod species as given by Tattersall, Elmhirst and Fage it is interesting to note that seven species are common to the lists of Tattersall and Fage, namely, *Metaphoxus pectinatus* and *fultoni*, *Synchelidium haplocheles*, *Perioculodes longimanus*, *Apherusa bispinosa*, *Dexamine spinosa* and *Guernea coalita*; five common to the lists of Elmhirst and Fage, namely, *Gammarus locusta*, *Bathyporeia* sp., *Pontocrates* sp., *Perioculodes longimanus* and *Paratylus swammerdami* (*Nototropis schwammerdami*); and but one only common to all three lists, namely, *Perioculodes longimanus*. Patience (1909) records *Metaphoxus pectinatus* and *fultoni* as occurring at night time in the waters of the Firth of Clyde, thus making three species common to all three areas. Several authors refer to the vertical migration of *Apherusa bispinosa*, *Dexamine spinosa* and *Guernea coalita* (see Fage, pp. 211, 218 and 233 respectively). Russell (1925) shows that samples, taken at various depths up to 50 m. in the waters of the English Channel on a moonlight night in July, contain various benthic amphipods belonging to the genera *Monoculodes*, *Bathyporeia* and *Ampelisca*. A species of the genus *Urothöe* was exceptional in being present in the surface waters at 9 p.m. He further shows (1927) that in a series of samples taken during the day truly benthic amphipods are absent except for species of the genus *Apherusa*, mainly *A. ovalipes* and *A. clevei*. Fish (1925) records, particularly, four species of amphipods in tow-nettings taken at Wood's Hole, *Batea secunda*, *Stenothöe cypris*, *Monoculodes edwardsi* and *Calliopus laeviusculus*, the two former breeding during the summer, the two latter during the winter, but does not distinguish between day and night migrants. He is doubtful of the extent to which nocturnal vertical migration affects the night population of amphipods in the surface waters. It is interesting to note, however, that of the twenty-six species of benthic gammarid amphipods listed, seventeen belong to families which also show night migrants in the lists of Tattersall and Fage.

Thus it may be stated that it is a feature of certain species of benthic amphipoda, particularly some of those belonging to the families Haustoriidae, Phoxocephalidae, Oedicerotidae, Calliopiidae, Atylidae and Dexaminidae, to perform nocturnal vertical movements. How far such movements are a normal feature of all the species in these families and whether such movement is spasmodic and of rare occurrence in other families, such as certain species in the families Lysianassidae, Ampeliscidae and Gammaridae, must remain a matter of interesting speculation pending much further detailed investigation.

The nocturnal vertical movement of pelagic amphipods, particularly the Hyperiidae, is well known from the work of Hardy & Gunther (1935) and also Barnard (1932) on the plankton samples of the *Discovery* Expedition, and the nocturnal vertical movement of macroplankton organisms in general from the work of Russell at Plymouth. It is unnecessary to review this literature in this paper since it is probable that such movement of planktonic organisms is of a fundamentally different nature.

A discussion of the factors which control this nocturnal vertical migration must remain largely speculative pending further detailed investigation. That the movement is not a feeding one seems fairly definite, since observations on *Bathyporeia*, as yet unpublished, show that they feed when lying buried in the sand by projecting sand particles on to the mouthparts and removing the particles of food that cling to the particles. Foxon (1936) also shows that the cumacean *Pseudocuma longicorne*, which lives in the same habitat, feeds in essentially the same way; in fact it is probable that all benthic littoral amphipods, mysids and cumaceans feed whilst associated with their sea-floor habitat. The association of the movement with the reproductive cycle is suggested by the concentration of adults as compared with young forms. The evidence given above for *Bathyporeia*, that given by Elmhirst (1932) for other amphipods in Kames Bay, and many of the species referred to by Fage (1933), shows that adults are predominant. The results given by Fage, however, mostly show a much higher percentage of adult males compared with my figures for *Bathyporeia*. This is probably due to the effect of the lantern in concentrating the adult males with their large eyes and in having a less effect on the adult females with their smaller eyes. Fage (1933), Foxon (1936) and Tattersall (1938) show that similar concentrations of adults as compared with young forms occur also in some mysids and cumaceans. Thus an explanation of this movement may, in part, be found to be associated with the breeding cycle. Foxon's suggestions that "it is unlikely that the formation of pairs would take place in the sand", and that the "function of the swarm is to enable the males and females to locate each other", will apply equally well to *Bathyporeia* and to the mysids, but it does not explain the presence of numerous immature forms in occasional samples. Tattersall suggests that the vertical movement of immature mysids is probably connected with environmental factors such as temperature, again a suggestion that will apply equally well to *Bathyporeia*. Fage shows that in certain species such as *Gammarus locusta* immature forms only are obtained. Thus it is probable that different factors may control the movements of adults and young immature forms. Foxon further suggests in connexion with *Pseudocuma longicorne* "that where swarms consisting entirely of males are formed, these are forming a swarm into which the females can enter and so find a mate", a suggestion which implies that the males occupy a higher level in the water than the females. This paper supplies no evidence that the males of *Bathyporeia* occupy a higher level in the water than the females, since the method of capture at the water's edge of the tidal flow does not permit of sampling at various depths, in fact all samples show a mixed population. From further data collected by Mr Elmhirst during 1932 and again during 1936, when samples were obtained at the surface and at a depth of 2 fathoms, it may be concluded that the *Bathyporeia* population is always a mixed one and no swarms consisting entirely of males occur. Fage, however, shows that in four species of the genus *Urothöe* no female or immature specimen was captured within or without the orbit of the light employed. Thus in certain species a factor which affects adult males only may have to be considered.

Foxon further suggests that "the females come to the surface when eggs are about to hatch so that the young may have the same opportunity of dispersal". Tattersall has made the same suggestion in regard to certain mysids. This suggestion does not account for the presence of adult males and implies that some females with well-developed embryos in the brood pouch would occur. No female with young in the brood pouch was taken throughout this series of samples, the numbers with eggs were relatively few, and the presence of small newly hatched forms in the samples which cannot have escaped through the meshes of the net is not indicated. However, from observations made by Mr A. K. Vaughan of the University College of Wales (as yet unpublished) on the life cycle of *Bathyporeia* on the Cardiganshire coast, it is known that the release of the young forms from the brood pouch takes place at the periods of new and full moon. Whether this fact bears a relationship to the increase in numbers in the tidal waters in the periods immediately preceding new and full moon must remain at the moment problematical.

The above discussion attempts to find factors controlling the nocturnal vertical movement of *Bathyporeia* almost entirely in relation to the breeding habits of the species; other factors, however, such as purely physical ones, should be considered. Wheeler (1937), in a discussion concerning the vertical movement of prawns off Bermuda, reaches the tentative conclusion that, of the factors controlling periodicity, light is the most likely one as inhibiting their activity. The evidence on *Bathyporeia* in this paper shows that periodicity in relation to the lunar cycle is a feature of the vertical movement of the species in this genus. That light is not a major controlling factor in the genus is shown by the fact that the numbers in the tidal waters increase in the periods immediately preceding new and full moon, but that it is a factor seems definitely indicated in that they do not occur in the tidal waters during the day time.

A reference to Table III shows that individuals were taken in all the months of the year with larger numbers in the samples from March to September than in the autumn and winter months. The largest samples were obtained in July, March, May and June in that order, so that temperature cannot be regarded as an important factor apart from the effect which it may have on the breeding cycle.

There remains the possible influence of the tides, which may be regarded as an important factor in an intertidal area. That this factor is of importance is shown by the increase in numbers in the two periods which correspond to the highest rises of the tide in each lunar month. It may be noted that the life cycle of *Bathyporeia* is such that each batch of eggs takes about 15 days to develop, hatch and be released from the brood pouch. In *B. pilosa* broods are produced all the year round, but with larger numbers breeding during the spring and summer months, with an occasional extensive brood during these months, which may account for the larger numbers in the samples at definite periods. It may be noted that *B. pilosa* appears in the samples all the year through. With *B. pelagica* breeding is confined to the spring and summer months, and it appears in the tidal waters apart from an occasional specimen during these months only. The results obtained by Fage (1933) and Fish (1925) show that certain species appear in the plankton for periods of time only, some are summer migrants, others winter migrants. Thus a knowledge of the period and length of the breeding cycle for each species is necessary. Clark (1925) has shown an interesting connexion between the tides and the breeding of the fish *Leuresthes tenuis*.

It appears that the nocturnal vertical movement of *Bathyporeia* into the waters of the tidal flow is determined, in part, by the influence of the tides which has some relation to the double breeding cycle in each month.

SUMMARY

The zonation of four species of the genus *Bathyporeia*, from high-water mark to low-water mark, in Kames Bay, Millport is given. *B. pilosa* occurs above the high-water mark of neap tides, *B. pelagica* is a mid-tidal form and *B. elegans* a low-water form. The latter, together with *B. guilliamsoniana*, extend beyond low-water mark. Of the population, as it occurs in the sand, 15% are adult males, 26% adult females, giving a proportion of adult to immature forms of 41 : 59.

The analysis of forty-five tow-net samples taken across the bay at night shows that the same zonation of the species is maintained; the proportion of adults to immature forms in these samples, however, is as 57 : 43, and of the 57% of adults, 42% are adult males, 15% adult females.

When the samples are related to the day of the lunar month it is shown that the numbers increase in the tidal waters in the periods immediately preceding the full moon and preceding and partly overlapping the new moon.

A nocturnal vertical movement appears to be a marked feature of a few benthic amphipod families, but the factors which cause this migration are problematical and require much further investigation.

REFERENCES

BARNARD, K. H., 1932. Amphipoda. *Discovery Reports*, Vol. v, pp. 1–326.

CLARK, F. N., 1925. The life history of *Leuresthes tenuis*, an atherine fish with tide-controlled spawning habits. *Cal. Fish and Game Com., Fish Bull.*, No. 10, pp. 1–51.

ELMHIRST, R., 1932. Quantitative studies between tide marks. *Glasgow Naturalist*, Vol. x, pp. 56–62.

FAGE, L., 1933. Pêches planctoniques à la lumière effectuées à Banyuls-sur-Mer et à Concarneau. III. Crustacés. *Arch. Zool. Expér. Gén.*, Tome 76, pp. 105–248.

FISH, C. J., 1925. Seasonal distribution of the plankton of the Wood's Hole region. *Bull. Bur. Fish. Washington*, Vol. XLI, pp. 91–179.

FOXON, G. E. H., 1936. Notes on the natural history of certain sand-dwelling Cumacea. *Ann. Mag. Nat. Hist.*, Ser. 10, Vol. 17, pp. 377–93.

HARDY, A. C. & GUNTHER, E. R., 1935. The plankton of the South Georgia whaling grounds and adjacent waters 1926–7. *Discovery Reports*, Vol. XI, pp. 1–456.

PATIENCE, A., 1909. On the genus *Phoxocephalus*. *Glasgow Naturalist*, Vol. I, pp. 116–34.

RUSSELL, F. S., 1925. The vertical distribution of marine macroplankton. An observation on diurnal changes. *Journ. Mar. Biol. Assoc.*, Vol. XIII, pp. 769–809.

—— 1927. The vertical distribution of marine macroplankton. V. The distribution of animals caught in the ring-trawl in the daytime in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XIV, pp. 557–608.

TATTERSALL, W. M., 1913*a*. Clare Island Survey. Amphipoda. Pt. 42. *Proc. Roy. Irish Acad.*, Vol. XXXI, pp. 1–42.

—— 1913*b*. Clare Island Survey. Nebaliacea, Cumacea, Schizopoda and Stomatopoda. Pt. 41. *Proc. Roy. Irish Acad.*, Vol. XXXI, pp. 1–10.

—— 1938. The seasonal occurrence of mysids off Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 43–56.

WATKIN, E. E., 1938. A revision of the amphipod genus *Bathyporeia*. *Journ. Mar. Biol. Assoc.*, Vol. XXIII, pp. 211–36.

WHEELER, J. F. G., 1937. Further observations on lunar periodicity. *Journ. Linn. Soc. London*, Vol. XL; pp. 325–345.

THE PHYSIOLOGY OF MATURATION AND FERTILIZATION IN *POMATOCEROS TRIQUETER* (L.) I. THE NATURE OF THE MATERIAL

By J. B. Cragg, M.Sc.

Assistant Lecturer in Zoology, University College of North Wales, Bangor

(Text-figs. 1–5)

While investigating the physiology of maturation and fertilization in the marine worm, *Pomatoceros triqueter*, it soon became evident that there was great variability in the reactions of the material, not only among the egg batches from different worms but even in the eggs liberated from one worm. For accurate interpretation of the results it was important that some knowledge of this variability should be obtained. This paper is therefore devoted to the individual and seasonal variations shown by the material.

Material

The animals were collected from the north side of Cullercoats Bay. The principal sources were the "Gut" and the hollow close to the north breakwater.

During the course of the work over 3000 worms were examined, the sex ratio being about five females to one male. The distribution of the sexes appeared to be haphazard, but the material was selected to give large numbers of eggs, large specimens forming the greater number of those examined. A statistical study of different size classes might show a reversal of sex in the animal or a size difference between the sexes.

Methods

The material for the studies on seasonal variation, carried out between September 1934 and September 1935, was collected the day prior to or on the morning of the experiment. For other work, apart from certain special cases to be referred to later, the material was never kept in the aquarium for more than three days before use.

To collect the germinal products the stone on which the animal had formed its tube was first washed with tap water, the tube chipped away, and the worm removed. If a female, it was quickly rinsed in tap water, then in Berkefeld filtered sea water, and finally placed in the dish of sea water or experimental solution in which the eggs were required. Since liberation proceeds very rapidly once the tube is broken, the above steps must be carried out quickly.

Practically complete liberation occurs within 10 min. of opening the tube. Uniform crystallizing dishes about 5 cm. in diameter and in depth were used for the experiments. No special precautions were taken to control the temperature, but records were kept throughout each experiment. The *p*H of the experimental solution was determined colorimetrically before and after each experiment.

Previous workers have usually paid little attention to the accuracy of results obtained from egg counts, although Fuchs (1915) working on *Ciona* drew attention to the possible errors associated with egg counts and the desirability of making check counts. The chief source of error in the present work was the difficulty of obtaining a uniform mixture of eggs for distribution to the various solutions. The best method was to shake the eggs thoroughly in 25 c.c. of solution and then by a rotary motion collect them in the centre of the dish. A fine pipette was then used to transfer the eggs. In filling the pipette eggs were collected from different regions of the egg mass and approximately the same number of eggs was present in each transfer. Counts were made in the dish, not by transfer to a slide which in itself introduces a source of error. Unfertilized eggs were fixed by the addition of formalin after a lapse of 4½ hr., for then practically all eggs capable of maturing had done so. Results had sometimes to be based on counts of only 300–400 eggs. The degree of accuracy of the method as tested by repeated countings was ±3% for mature eggs and fertilization stages and ±10% for immature oocytes.

Males were transferred immediately to about 5 c.c. of sea water instead of being washed in tap water. After liberation of the sperm the worm was removed and the mixture shaken. When more than five batches of eggs had to be fertilized the method advised by Fuchs for making a sperm suspension proved more satisfactory; that is, to dilute the original suspension and ensure thorough mixing by pouring the liquid from one vessel to another about twenty times. Fertilizations were made by adding one or more drops of sperm suspension and fertilized batches were fixed 5 hr. after the addition of sperm.

The Form of the Egg

When shed from the worm the eggs are primary oocytes (Fig. 1) and they are usually light red in colour. Each egg possesses a large, clear germinal vesicle, the diameter of which is half that of the egg. A large asymmetrically placed nucleolus is present in each nucleus. The cytoplasm is finely granular, with the granules evenly distributed. The egg is surrounded by a vitelline membrane 2 μ in thickness, the surface of which is covered by a system of fine furrows or indentations. By cytolysing eggs in distilled water the membrane was shown to be very tough. When liberated the eggs are usually irregular or flattened. The mean diameter of flattened eggs, based on measurements of 50–100 eggs, varies with the batch. In the majority it is 65–70 μ, but eggs giving a mean diameter of over 80 μ have been recorded.

A varying percentage of the eggs liberated, depending on the ripeness of the batch, mature. This change is characterized by the breakdown of the germinal vesicle, the egg becoming purple-red in colour and approximately spherical. The mean diameter of such eggs was 63–68 μ. A comparison of the measurements of flattened primary oocytes and mature eggs indicates the marked variation in the form of the primary oocyte (Fig. 2). The change from primary oocyte to mature egg took place mainly in the 4 hr. following liberation; longer intervals in sea water without fertilization resulted in cytolysis. The common cytolytic form superficially resembled the blastula stage of a fertilized egg. The earliest time for the appearance of these "pseudoblastulae" was 6 hr. after liberation, but their formation depended on the ripeness of the material. Ripe material, that is a batch of eggs giving a high percentage of mature eggs, would show complete cytolysis 24 hr. after liberation. In an unripe batch this was delayed, some fertilizable primary oocytes remaining 80 hr. after liberation.

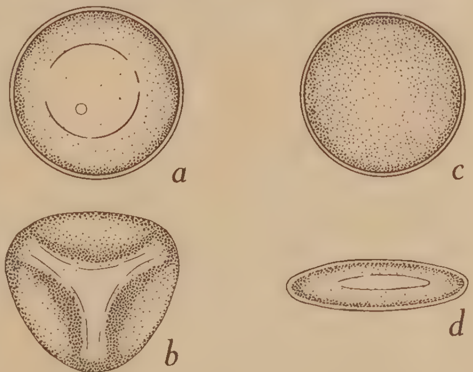


Fig. 1. *a*, flattened primary oocyte viewed from above, showing the germinal vesicle with excentric nucleolus; *b*, misshapen primary oocyte, this is the usual appearance of eggs after liberation; *c*, an egg which has matured; *d*, flattened primary oocyte viewed from the side, this corresponds to the form described by Hörstadius.

These observations do not agree with the description of the material given by Hörstadius (1923). He considered that the primary oocytes were flattened and that, after breakdown of the germinal vesicle, the long diameter decreased and the breadth increased but the egg did not become spherical. The flattened forms are, however, not of one shape. Only extremely flattened eggs agree with Hörstadius's description of the primary oocyte. In no case did the mature egg resemble the stage described by Hörstadius. In the first place, it tended to become approximately spherical. Secondly, from both the figure and the description it should have shown a prominent perivitelline space; this could not be observed. By treating mature eggs and even fertilized eggs with hypertonic sea water the withdrawal of the egg protoplasm from the vitelline membrane could be watched, giving clear evidence that no perivitelline space existed before or after fertilization.

Hörstadius also stated that the eggs underwent a reduction in volume on reaching maturity. In view of the large variation in shape, such a conclusion cannot be arrived at from measurements of the long and short diameters of primary oocytes and mature ova.

Under the conditions of liberation which existed in these experiments the eggs were accompanied by a varying number of immature oocytes. The smallest of these are colourless, but as size increases the colour approximates to the light red of the primary oocyte. They can, as a rule, be distinguished from primary oocytes by a zone free from granules beneath the vitelline membrane.

The rounding off of eggs has been attributed to a change in permeability. In both *Asterias glacialis* (Dalcq, 1923, 1924) and *Sabellaria vulgaris* (Waterman, 1936), where such an explanation has been advanced, rounding off occurs immediately on contact with sea water and the germinal vesicles remain intact. In *Pomatoceros* conditions appear to be different. Mere liberation into sea water is not enough to produce rounding off; some eggs even after 24 hr. in sea water may still be misshapen. Here, rounding off is associated with the breakdown of the germinal vesicle. At first it appeared as though certain eggs with complete germinal vesicles also underwent the change, but, since such eggs were darker in colour than the unchanged primary oocytes, it is probable that the nuclear membranes whilst visible were not intact.

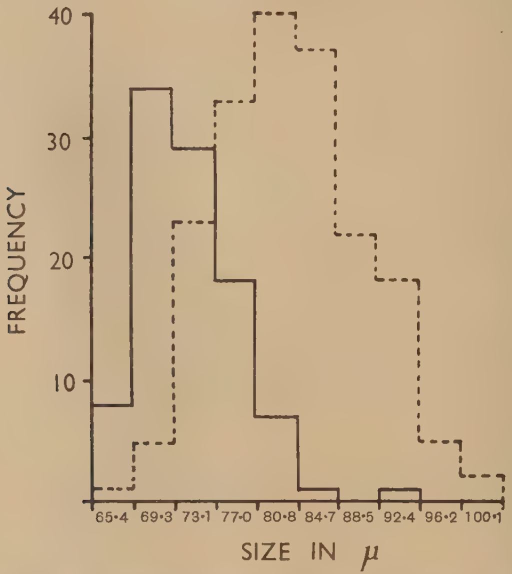


Fig. 2. A comparison of the variations in diameter of primary oocytes with eggs of the same batch which have matured. Mature eggs ———, primary oocytes – – – – – – – –. A marked reduction in diameter is associated with this change and is due to the eggs rounding off. Primary oocytes 82·2 μ ± 6·8. Mature eggs 72·8 μ ± 4·7.

In animals such as *Pomatoceros*, where it is not an immediate phenomenon following liberation into sea water, rounding off can be explained without assuming a change in permeability. Hobson (1932) indicated that the vitelline membrane had elastic properties. If such a membrane were distorted owing to the combined effects of the eggs being packed tightly in the body cavity and being forced out of a slit-like aperture on liberation, it would tend to return to its normal form unless some opposing force were exerted on it. Such resistance would exist if the egg protoplasm was in a very viscous condition. If, on maturing, the viscosity decreased or movements took place in the protoplasm, the elastic properties would result in the egg becoming spherical. Evidence from other species suggests that such changes might occur. Harris (1935) has recorded marked streaming movements and a large drop in viscosity following the breakdown of the germinal vesicle in eggs of *Sabellaria alveolata*. In *Nereis* (Hoadley, 1934) the internal changes associated with the disappearance of the germinal vesicle are so violent that distortions occur in the shape of the eggs.

The Normal Course of Maturation and Fertilization

Maturation is not completed before fertilization. The egg can progress as far as the breaking down of the nucleus, but it must await insemination before the polar bodies are liberated. It is therefore like the majority of annelids, molluscs and echinoderms other than certain echinids.

In ripe eggs, the spermatozoon enters within 5 min. of adding the sperm, and, if it has not already done so, the germinal vesicle breaks down and the egg becomes spherical. Normally no membrane is raised on fertilization, although in exceptional cases a perivitelline space may appear at one or more points. No change was noticed in the attachment of the membrane to the egg surface until the polar bodies were liberated. Then the membrane was stretched in the region where the polar bodies lay and its internal and external limits could be clearly seen. There is nothing to suggest that the membrane is in any way different from the vitelline membrane of the unfertilized egg. An observation which pointed to the polar bodies being attached to the membrane was made when treating fertilized eggs with hypertonic sea water. The egg protoplasm withdrew from the membrane, but the polar bodies remained attached to both membrane and egg surface, being drawn out between them.

The minimum time for the disappearance of the nuclear membrane and the appearance of uniformity of colour in the egg was 6 min. at 16° C. The two polar bodies were liberated at about 30 and 50 min. respectively. There was no reconstitution of the pronucleus and the eggs reached the first cleavage after an interval of about 100 min. These figures are only approximations, for a considerable amount of variation occurs.

Variation in the Material

Variations in the physiological condition of the eggs liberated from different worms were often recorded. There was a wide range of variation in the percentage of unfertilized eggs which matured. In fertilized eggs there might be present at the same time two- to eight-cell cleavage stages. In addition there might be a number of eggs into which sperm had penetrated, but which had not undergone division. It was an exception to find a batch of eggs which proceeded through the various cleavage stages as uniformly as is found in the majority of echinoderms. Evidence of variability was also brought to light in the experimental studies.

Variation in the Degree of Maturity

It was thought that the number of unfertilized eggs which matured would be a measure of the ripeness of the material. An attempt was made, therefore, to see whether the degree of maturity was directly related to fertilizability, as measured by the proportion of eggs undergoing cleavage. The procedure was to fertilize ten batches of eggs with sperm from the same male, an unfertilized control series being kept. These experiments failed to show that such a relationship existed.

Variation in Individual Egg Batches

The egg batch of one worm could be divided up by allowing the worm to remain in one dish only for a short time, after which it was transferred to another, and so on through a series of dishes. In general, it was found that the number of mature eggs was highest in the batches liberated last (Fig. 3). With the gradual rise in the number of mature eggs there was a sharp drop in the total number of eggs and immature oocytes (Table I).

TABLE I. TYPICAL SERIES OF RESULTS OBTAINED BY THE TRANSFER METHOD

The time of transfer given in column 1 is the time of removal of the worm from one dish to the next in the series.

Time of transfer	No. of eggs liberated	No. of immature oocytes	No. of eggs lib./sec.	Immature oocytes lib./sec.
15 sec.	8800	340	587	23
30 ,,	2400	440	160	29
40 ,,	780	180	78	18
1 min.	740	60	37	3
2 ,,	740	30	12	0·5
3 ,,	780	120	13	2
4 ,,	800	90	13	1
8 ,,	1160	100	5	0·4
16 ,,	1650	150	4	..
16+ min.	1150	200	..	..

Such transfer series, by providing fractions more uniform in themselves with respect to maturity than a complete egg batch, allowed further tests to be made regarding a relationship between maturity and subsequent cleavage. These experiments showed that the increase in maturity common in transfer experiments could sometimes be associated with increased cleavage (Table II).

Whilst the difference in the degree of cleavage between the units of a transfer series might be negligible, it should be noted that on no occasion did a unit with few mature eggs give a cleavage value significantly higher than that given by a unit containing a greater proportion of mature eggs. In the experiments where whole batches were used it was quite common to find that batches with few mature eggs gave better fertilizations than others apparently more mature. It is evident from the difference in behaviour between units in a transfer series and complete egg batches, that it would be possible for fundamental physiological differences to be veiled by utilizing data gained only from experiments using the whole egg batch as a unit.

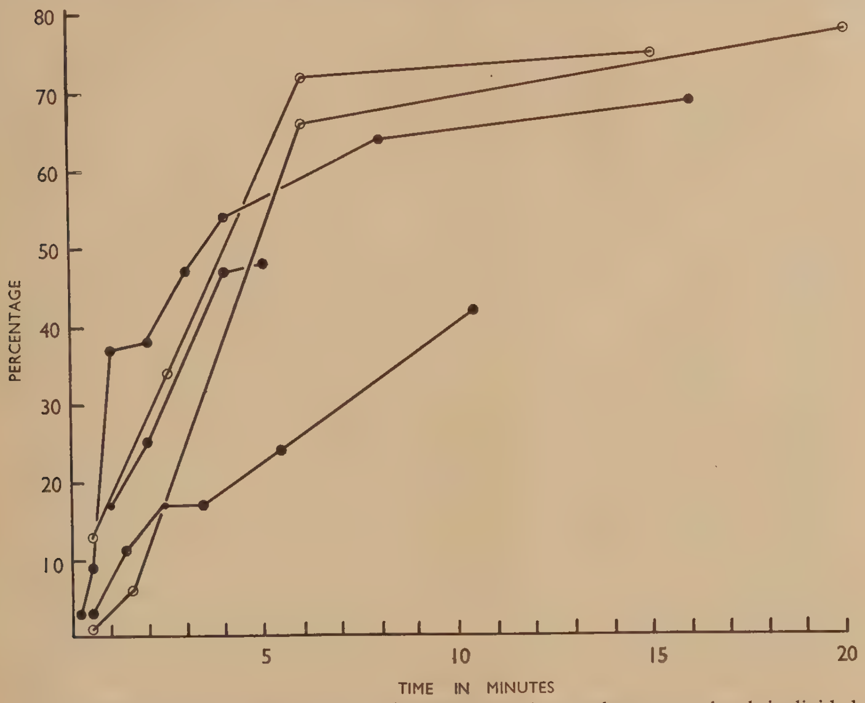


Fig. 3. The increase in the percentage of mature eggs shown when an egg batch is divided up into a number of units by the transfer method. The percentage of mature eggs in a unit is recorded against the time at which the worm was transferred from that unit.

The mechanism whereby unripe material is liberated first has not yet been elucidated. It may be dependent on the relative positions of the unripe germ cells and the segmental openings. Certainly this liberation of unripe and then ripe eggs does not result from a linear distribution in the body cavity according to ripeness. For in a series of nineteen experiments in which worms were cut in half, nine showed the anterior region to contain the higher percentage of ripe eggs and four the hinder region.

TABLE II. TRANSFER EXPERIMENTS SHOWING THE RELATIONSHIP BETWEEN MATURITY AND CLEAVAGE

The percentage of mature eggs in the unfertilized sample and the percentage cleavage after fertilization are given for each transfer unit.

	Transfer units					
Mature eggs	0	9	29	..	..	..
Cleavage	25	32	68	..	..	..
Mature eggs	1	2	1	24	..	..
Cleavage	8	9	14	24	..	..
Mature eggs	4	6	9	9	14	20
Cleavage	49	47	52	51	55	58

NATURAL SPAWNING

In view of the heterogeneity of the eggs liberated when the tube is opened, attention was turned to the possibility of collecting naturally spawned eggs. The aim was to see whether, in natural liberation, the eggs are more homogenous and whether the immature oocytes, which in artificial liberations are discharged first, are conserved.

Stones with one or more worms were kept in separate finger bowls, partially immersed in an aquarium tank and aerated. They were examined daily for signs of spawnings and, since none occurred, were opened after being two months in the aquarium. They contained high percentages of cytolysed eggs and yielded poor fertilizations. In one sample 50% were cytolysed and only 10% of the remainder were capable of fertilization; these, however, gave normal larvae. A characteristic of many of the eggs was the occurrence of vacuoles in the cytoplasm; as many as five were noted in some of the eggs. This condition was also shown by worms which had been kept in the aquarium tanks for the same period. The presence of large numbers of cytolysed eggs was common during the first three months of these artificial conditions. After that, some of the worms showed complete absence of germinal products, others showed a few normal primary oocytes and were quite free from cytolytic forms. After five to ten months a very significant change had occurred. Compared with the fresh material from the shore the egg content was about ten times as great; egg batches of 10,000–40,000 eggs being the rule. This tank material was quite normal and made possible experiments of a size which had hitherto been impracticable. Since all the worms kept in these artificial conditions contained a large store of eggs or sperm and since no natural spawnings were observed, the state must have arisen from continual production with non-liberation.

SEASONAL VARIATION

Very early in the work it was found that the possibility of obtaining a good batch of eggs, from the point of view of numbers and fertilizability, varied during the month. Daily records of maturity and cleavage were kept. In view of the fact that the results did not reveal any definite periodicity the observations were extended to include the percentage of immature oocytes, the number of eggs, the relative proportions of the different cleavage stages, and the relative numbers of ripe and unripe females.

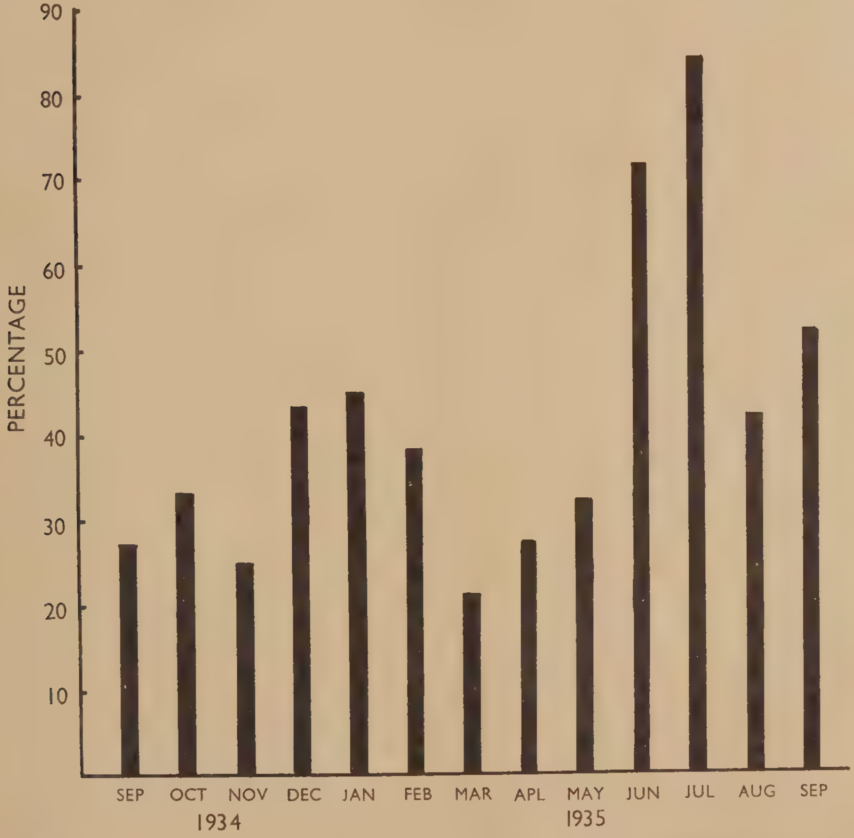


Fig. 4. The variation in cleavage throughout the year, as shown by the percentage of samples giving a cleavage value of or greater than 80 %.

No definite lunar periodicity was found. The immature oocytes, which were only recorded over a period of three months, showed no signs of a periodicity.

As regards mature eggs and cleavage there was a slight tendency for the highest values to occur about the time of the full moon, but this was not definite. The cleavage results showed a period lying between the full moons of June and July of consistently high values. This June–July deviation cannot be attributed to the existing laboratory or sea temperatures for similar temperature variations occurred at other times. The general trend of the observations suggests it to be a period of special breeding activity, although the possibility of fertilization exists throughout the year (Fig. 4).

VARIATION IN MATURITY

Whilst the data referred to above failed to demonstrate a lunar periodicity, they served a more positive purpose in that the frequency distributions of percentages of immature oocytes and of mature eggs indicated the nature of the change undergone in the transformation of an immature oocyte into a mature egg.

In the maturity distribution (Fig. 5) it will be seen that the major class consists of egg batches containing 0–10% mature eggs. The distribution of immature oocytes (Fig. 5) is that of a skewed normal distribution. The skew is probably the result of the technique, for it was essential to obtain enough eggs for fertilized and unfertilized samples. When the number of immature oocytes was large, in particular over 90%, the material was rarely used. The difference between the two distributions, especially when it is remembered that the mature egg is only the later stage of the immature oocyte, is remarkable. There are two possible explanations for the peculiar form of the maturity distribution.

1. That eggs are liberated as they ripen, the actual time of liberation depending on certain variable conditions. In such circumstances most females opened would show a majority of unripe eggs and the immature oocytes would be fairly constant in number.

2. That complete liberation occurs just prior to maturity, the form of the frequency distribution of maturity arising from the nature of the reactions producing maturity. If the development of maturity were dependent on a series of chemical or physical changes whose rate after initiation gradually increased, then the interval passed by a batch in the 0–10 stage would be longer than that passed in the more mature conditions. Very mature batches would, therefore, be rarely found.

The second hypothesis appears to be the more probable. The frequency distribution of immature oocytes is in keeping with it and militates against the first hypothesis. Also, the total number of eggs liberated show marked fluctuations not in keeping with the idea of gradual liberation.

VARIATION IN MATURITY THROUGHOUT THE YEAR

Table III shows the monthly variations in maturity. There was a gradual decrease in the number of higher maturity groups present as the summer months approached, culminating in July where the 0–10 class predominated. In August the higher classes again increased.

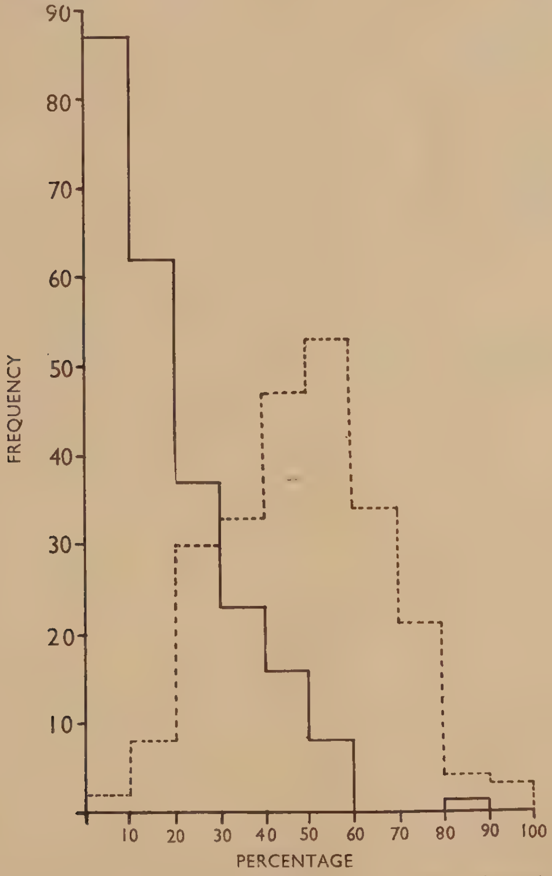


Fig. 5. A comparison of the immature oocytes and mature egg values given by the same material. Mature eggs ————, immature oocytes – – – – – – – –. Data collected June 21 to September 17 1935.

It is improbable that this monthly variation is wholly a result of the individual experiments being carried out at existing laboratory temperatures, which varied throughout the year. This conclusion is supported on the following grounds. Hörstadius has shown that up to 16° C. the percentage of mature eggs increases with rise in temperature. Above that temperature there was a decrease and at 22° C. 81 % of the eggs were deformed. If the present results arose principally from the effect of temperature at the time of the individual experiments, then the data when classified on a temperature basis should show the higher maturity values increasing with rise in temperature up to 16° C. and then decreasing. As will be seen by reference to Table IV, where the data have been reclassified, this is not so. Also, experiments to see the effect of allowing parts of the same egg batch to mature at different temperatures have shown that summer material can develop, without cytolysing, at higher temperatures than winter material (the degree of resistance of eggs to warmth depends on a number of factors and is at present being investigated). It seems reasonable to conclude, therefore, that whilst the temperature at which the experiment is conducted will undoubtedly influence the degree of maturity, it is not the principal factor concerned in producing the variation already outlined.

TABLE III. MATURITY DETERMINATIONS

This table gives the results of all maturity determinations made under standard conditions. The individual maturity percentages are classified in groups differing by 10 %, the number of results in each group being expressed as a percentage of the total number of determinations made during the month.

Month	Percentage maturity groups										Total no. of results
	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	
Dec. 1934	22	15	30	11	15	4	..	..	4	..	27
Jan. 1935	19	21	17	15	15	6	4	2	..	..	52
Feb.	29	33	19	14	..	..	..	5	..	..	21
Mar.	24	51	18	3	3	..	..	..	..	..	33
Apr.	25	33	21	4	8	4	4	..	..	..	24
May	38	28	24	7	..	3	..	..	..	..	29
June	33	28	20	9	2	4	2	..	..	2	46
July	52	19	15	2	7	4	..	..	..	..	80
Aug.	34	24	19	13	9	1	..	..	..	..	79
Sept. 1–17	24	35	12	16	4	8	..	..	..	..	49

TABLE IV. MATURITY VALUES CLASSIFIED ON A TEMPERATURE BASIS

The results are classified according to the mean temperatures of the experiments. The number of results in each percentage maturity group has been expressed as a percentage of the total number of results in that particular temperature group.

Temperature ° C.	Percentage maturity groups										Total no. of results
	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	
9·9–10·8	32	48	4	4	4	..	4	4	..	..	25
11·0–12·9	24	24	22	14	7	4	2	1	..	..	90
13·0–14·9	25	24	32	7	5	7	..	..	1	..	76
15·2–16·8	27	31	17	13	6	3	1	..	..	..	96
17·3–17·8	45	26	11	6	10	..	..	..	..	2	62
19·0–21·0	43	23	14	7	9	4	..	..	..	..	91

On p. 492 a hypothesis has been advanced to explain the form of the maturity frequency distribution. The variation in the monthly classes would signify an acceleration in the speed of the reactions concerned. Such an increase in the rate of production of ripe eggs would explain the gradual disappearance of the higher maturity values during the summer months.

Discussion

The description of the eggs of *Pomatoceros* given here differs in certain respects from that of Hörstadius. Whilst the explanation might be that the earlier observations were based on a relatively small sample of eggs, the possibility of fundamental differences between the material at Cullercoats and at Kristineberg must be borne in mind.

From the viewpoint of cell permeability shape changes in eggs are of special importance, for it has been usual to treat the egg as spherical when calculating volume change. If the changes recorded here and by Hörstadius were of general occurrence then much of the work done on egg permeability would be vitiated.

The danger of static and dynamic variability leading to confusion in biological work, especially in cytological experiments, has been emphasized (Gray, 1931). Yet quantitative examinations of variability in populations of germ cells are few, although innumerable qualitative references occur in the literature of experimental cytology. A series of investigations by Goldforb has done much to record variability in the sea urchins, *Toxopneustes*, *Hipponoe* and *Arbacia*. The characters studied (Goldfarb, 1917) were size, shape, number of eggs with or without jelly layer, rate of membrane formation, and number and rate of cleaving eggs. These characters were held to be correlated and by knowing certain of them the behaviour of a batch of eggs could be forecast. Goldforb repeatedly asserts that exact forecasts of the physiological condition of eggs could be made, but his results do not always support this view. When studying the variation in agglutinating power of egg waters (Goldforb, 1929), the results given consideration are not the agglutinating times of sperm based on individual samples of egg water, but averages of the individual results. Fundamentally, it is equivalent to using mixed batches of eggs. The individual results (see tables II*a* and II*b*, Goldforb, 1929) used to give the averages often show marked differences. In one an average of 115% is obtained by averaging 300, 50, 112 and 0% (these figures represent percentage increase in agglutinating time after the egg batches have been kept for a common time). These average results are held to show "...progressive and marked increase in agglutination time with ageing of eggs". Such results indicate that whilst a trend towards "poor" and "good" might be obtained, individual batches could not be classified as such with any accuracy prior to carrying out the experiment.

Grave (1928) working on *Cumingia tellinoides* and Grave & Oliphant (1930) on *Hydroides hexagonis* record variations in the physiological condition of the germinal products, but no attempt at such a definite analysis as that of Goldforb is made.

Dalcq (1928) showed that in *Barnea candida* an increase in maturity could be produced by increasing the concentration of the potassium or calcium ion in the basic physiological solution. The relationship was in the form of a sigmoid curve. The explanation advanced was that the eggs leaving the ovary were not in a uniformly ripened series, but contained a major class which responded to a certain concentration.

Both Goldforb and Grave & Oliphant consider the poorest lot of eggs to be those giving the most rapid disintegration. This criterion is open to question. Grave & Oliphant use as their standard for disintegration two types of cytolysis. One of these, from their descriptions, bears a striking resemblance to the "pseudoblastulae" cytolysis of *Pomatoceros*. Now, in *Pomatoceros*, eggs which mature are the first to give rise to pseudoblastulae. A batch of eggs maturing rapidly after liberation will give rise to the cytolytic form before a batch of primary oocytes, although they need not be in an inferior physiological condition.

None of the work quoted offers any means whereby the effects of variation can be cut out or rendered more manageable. Fry (1936) describes a method for obtaining egg batches of common cleavage times in *Arbacia*. It amounts to carrying out tests on several batches of eggs and finding those with the same cleavage time. Such batches are then mixed and used for experiments. The problem is not so simple in *Pomatoceros*, for in this species it is clearly evident that the degree of variability among batches, especially where comparison is to be made among fertilized batches, is such as to prevent adequate knowledge of the processes leading to maturation being obtained from experiments on the whole egg batch. This variability is present in other marine worms also, for Grave & Oliphant record that for *Hydroides* "The variation in longevity within a single lot of eggs is greater than in the case of other species studied to date". Fortunately in *Pomatoceros* it is possible to divide up the egg content of a female into more uniform parts. The transfer series, as well as reducing the unwieldly extent of static variability, offers a means of studying eggs of different growth periods, which at least are uniform in that they have developed within a common environment. The use of this method can undoubtedly be advanced to the study of other worms. One drawback which exists in its application is the small size of the egg batch.

The problem of natural spawning is important, for it is in terms of the eggs so liberated that the results should be interpreted. In animals like *Pomatoceros* where primary oocytes can be successfully fertilized, it is not essential that naturally spawned eggs should be on the point of maturing. In view of the fact that the worm is capable of giving fertilizable eggs at all times of the year and that no knowledge of communal spawning exists, it is possible that liberation occurs before complete ripeness of the batch. In those circumstances the fertilizable life of the egg would be longer and the chance of fertilization greater than if it were liberated on the point of maturity.

The greater part of this work was carried out at the Dove Marine Laboratory, Cullercoats, during the tenure of a post-graduate studentship awarded by Armstrong (now King's) College, Newcastle-on-Tyne. I wish to acknowledge assistance given by the staff of that laboratory, especially Prof. A. D. Hobson under whose direction the investigation was made.

SUMMARY

The description of the material used in the present investigation does not conform with that of Hörstadius. Attention is drawn to this lack of agreement.

A hypothesis based on viscosity changes within the egg has been advanced to explain the rounding off of eggs in sea water.

By means of what is called the transfer series the egg batch has been divided into a number of parts; the last liberated eggs being the ripest. The occurrence of large numbers of egg batches giving low maturity values has been attributed to maturity resulting from a series of changes whose rate after initiation gradually increases.

Attention is drawn to seasonal changes in the reactions of the germinal products. No definite lunar periodicity is shown in the ripening of the eggs.

REFERENCES

DALCQ, A., 1923. Recherches sur la physiologie de l'œuf en maturation. *Arch. Biol. Liége*, Vol. 33, p. 79.

—— 1924. Recherches expérimentales et cytologiques sur la maturation et l'activation de l'œuf d'*Asterias glacialis*. *Arch. Biol. Liége*, Vol. 34, p. 507.

—— 1928. Le rôle du calcium et du potassium dans l'entrée en maturation de l'œuf de pholade (*Barnea candida*). *Protoplasma*, Tome 4, No. 1, p. 18.

FRY, H. J., 1936. Studies of the mitotic figure. V. The time schedule of mitotic changes in developing *Arbacia* eggs. *Biol. Bull.*, Vol. 70, p. 89.

FUCHS, H. M., 1915. Studies in the physiology of fertilization. *Journ. Genet.*, Vol. 4, p. 215.

GOLDFARB, A. J., 1917. Variability of eggs and sperm of sea-urchins. *Publ. Carneg. Instn.*, No. 251, p. 71.

GOLDFORB, A. J., 1929. Changes in agglutination of ageing germ cells. *Biol. Bull.*, Vol. 57, p. 350.

GRAVE, B. H., 1928. Vitality of the gametes of *Cumingia tellinoides*. *Biol. Bull.*, Vol. 54, p. 351.

GRAVE, B. H. & OLIPHANT, J. F., 1930. The longevity of unfertilized gametes. *Biol. Bull.*, Vol. 59, p. 233.

GRAY, J., 1931. *Experimental Cytology*. Cambridge.

HARRIS, J. E., 1935. Studies on living protoplasm. I. *Journ. Exper. Biol.*, Vol. 12, p. 65.

HOADLEY, L., 1934. Pulsations in the *Nereis* egg. *Biol. Bull.*, Vol. 67, p. 484.

HOBSON, A. D., 1932. On the vitelline membrane of the egg of *Psammechinus miliaris* and of *Teredo norvegica*. *Journ. Exper. Biol.*, Vol. 9, p. 93.

HÖRSTADIUS, S., 1923. Physiologische Untersuchungen über die Eireifung bei *Pomatoceros triqueter*. *Arch. Mikr. Anat.*, Bd. 98, p. 1.

WATERMAN, A. J., 1936. Membranes and germinal vesicle of the eggs of *Sabellaria vulgaris*. *Biol. Bull.*, Vol. 71, p. 46.

SUBSTANCES CONTROLLING THE GROWTH OF A DIATOM

By H. W. Harvey, Sc.D.

Hydrographer at the Plymouth Laboratory

The centric diatom *Ditylum brightwelli* Ehrb. is found in the English Channel during the spring and autumn; in common with many other species it "dies out" during the summer months.

Its life history has been investigated by Gross (1937*a*) who used for this purpose cultures in sterilized sea water enriched with nitrates, phosphates and soil extract, a culture medium known as "Erdschreiber" (Gross, 1937*b*). The succession of events in its life history may be epitomized as follows. The cells make vegetative divisions for a period of several months, the successive generations of daughter cells becoming narrower. Under some conditions, such as crowding, low temperature and low light-intensity, the contents of a cell may retract into a sphere (resting spore) within the skeleton, and, on change of conditions, this resting spore will grow to refill the parental skeleton. This can happen within a few hours if conditions become suitable soon after the formation of the resting spore. Normal vegetative growth then continues. After many divisions have taken place, with consequent reduction to a certain diameter, the cells become capable of forming auxospores; this takes place under certain conditions of environment, and, if it does not take place, vegetative division continues. This may continue, no auxospores being formed, until the diameter of the cells falls to 10–13 μ, when they die. On the other hand, if auxospores are at any time formed, then either one of two things happens. If the environment is unsuitable the auxospores do not develop but perish; if the environmental conditions are suitable the auxospores develop into broad cells with diameters up to 100 μ, several times broader than the parent of the auxospores. These broad cells after several months of vegetative division, and reduction in size, again become capable of forming auxospores.

Gross found that formation of auxospores was, *inter alia*, brought about by transferring the cells from "Erdschreiber" into natural sea water, but that in sea water the conditions were unsuitable for their further development and they perished.

I am indebted to Dr Fabius Gross for a subculture of this diatom in "Erdschreiber". During the late summer and early autumn of 1937, I found that when it was transferred to natural sea water enriched with nitrates, phosphates, silicates and iron, most of the cells formed auxospores which did not develop and the remaining cells did not make vegetative divisions. The inability of auxospores to develop in natural sea water collected in the summer was not solely due to lack of phosphates, nitrates, silicates and iron. If a small quantity of soil extract was added to the enriched natural sea water, an inoculum of actively dividing diatoms would continue to grow vigorously by vegetative division. This happened repeatedly. It was found that the soil extract could be replaced by an extract of *Fucus* or of *Ulva* which had been allowed to undergo bacterial breakdown and had been separated from the bacteria and colloids by dialysis.

Sea water collected in late October 1937 behaved quite differently from sea water collected during the summer. When this was sterilized and enriched to the same extent with phosphates, nitrates and iron, the diatoms would grow in it without any further addition of soil or algal extract. This was found to happen with samples of water collected from time to time throughout the winter of 1937 and spring 1938.

Meanwhile a second strain of this species was grown from a single cell isolated from the sea in April 1938. It made considerable growth in water collected during the spring and during the previous winter, enriched with nitrates, phosphates and iron. In water collected during July 1938, similarly enriched, both strains formed auxospores which did not develop.

The inference drawn from these observations on growth in natural sea water is that these two particular strains of *Ditylum brightwelli* require for continued growth, not only a supply of available nitrogen, phosphate and iron, but, in addition, some other accessory substance or substances, whose concentration in offshore sea water was less than the necessary limit during the summer of 1937 and 1938. In the autumn of 1937 either the accessories were re-formed or a body of water containing the accessories had moved into the area. This "*fertile water*" either lost its fertility or was gradually replaced during the early summer of 1938. Samples of offshore water collected during the autumn and winter of 1938 behaved in the same way as water collected during the summer—there was no return of "fertile water".

Accessory substances are not necessary for the growth of all species of marine diatoms. Indeed, the pennate diatom *Nitzschia closterium* forma *minutissima* has been found capable of continued growth in synthetic media free from organic matter (Peach & Drummond, 1924). Originally isolated by Allen & Nelson (1910) it has had widespread use in many laboratories, and is remarkable for the ease with which it may be kept in culture in natural sea water enriched with nitrate, phosphate and iron. However, it has been repeatedly observed that if soil extract or an algal extract is added to the enriched sea water, the rate of growth is markedly increased. This happens even if the water is heavily loaded with both iron and silicate in addition to nitrate and phosphate (Harvey, 1933). With this *Nitzschia*, the accessory substances do not act as nutrients *necessary* for growth, as they do for the two strains of *Ditylum*, but they act as a growth stimulant.

Throughout this investigation, the natural and artificial sea waters used in the experiments were enriched with 30 mg. nitrate N, 3 mg. phosphate P and *ca.* 0·1 mg. Fe as ferric ammonium citrate per litre. The quantities of nitrogen and phosphorus added are in similar proportion to each other as they are in diatoms, are sufficient for the growth of several thousand *Ditylum* cells per c.c., and are in the region of optimum concentration. The amount of iron added was considered to be in gross excess of requirements, provided it remained available (Harvey, 1937).

It was thought that silicate occurring in the various extracts which were added in the experiments might have affected growth, but experiments did not show this to be so, sufficient being derived from the glass vessels. Later, when a means of producing very luxuriant growth had been discovered, it was found necessary to add silica if more than a few thousand cells per c.c. were to develop in the culture medium.

The method used in carrying out the biological tests was to transfer *Ditylum* cells from an *actively dividing* culture to the medium used for the control, collect them by centrifuging or allowing to sediment, again suspend them in the medium and sediment, then suspend them once more in the medium and use equal volumes of this to inoculate equal volumes of the control and experimental media. The cells were then kept, either at room temperature or at 13° C., where they received nearly equal illumination, but no direct sunlight. When relatively small differences in growth rate or final "crop" were to be observed, the glass vessels were kept on a slowly rotating table, so that they averaged equal illumination, and in order that the "lens effect" in the cylindrical vessels should be eliminated.

Growth in Artificial Sea Water

Allen (1914) found that the diatom *Thalassiosira gravida* would make no growth in an artificial sea water made with glass-distilled water and pure chemicals, providing chloride, sulphate, sodium, potassium, magnesium and calcium in the proportions in which they occur in sea water, with the hydrogen-ion concentration adjusted with bicarbonate and enriched with phosphate, nitrate and iron. The further addition of bromide and iodide was without effect, but, if a very small proportion of natural sea water or of a boiling water extract of *Ulva* was added, then a rich growth of this diatom took place.

From a long series of experiments he concluded that natural sea water contained a substance or substances of organic nature which was necessary for the growth of this diatom.

Peach & Drummond (1924) investigated the growth of *Nitzschia closterium* forma *minutissima* in similar artificial sea water and found that this species would grow without any addition of accessory substances. This species appears unique among marine diatoms for the adverse conditions, fatal to other species, which it will withstand. Allen (private communication) repeated Peach & Drummond's experiments with similar result, but observed that better (more rapid) growth was brought about by the addition of a small proportion of natural sea water or of *Ulva* extract. It has been repeatedly observed by the writer that the addition of such extracts hastens the growth of *Nitzschia*, even in sea water heavily enriched with inorganic nutrients.

A similar "artificial sea water" was made and enriched with nitrate, phosphate and iron. Neither strain of *Ditylum* would grow in it. With the addition of 5 % of natural winter sea water a rather poor growth resulted, while with the addition of soil or of algal extracts a considerable growth took place. The very small additions, which had been found by Allen to suffice for the growth of *Thalassiosira*,* were insufficient for the growth of *Ditylum*.

It is thought that the *Nitzschia* species can itself make the organic accessories which it needs for continued growth, that is to say that the accessories are of the nature of phytohormones. In support of this hypothesis are the observations that addition of "accessories" to the water causes more rapid growth, and an observation that it grows more rapidly in water in which the species has been growing previously (Harvey, 1933).

Experiments on the growth of *Ditylum* soon showed that the active principles which are present in soil extract and in algal extracts could be separated into two groups. The one, which will be termed group "A" accessories, was readily adsorbed on carbon and was insoluble in aqueous butyl alcohol. The other, group "N" accessories, was not adsorbed on carbon and was soluble in aqueous butyl alcohol.

The addition to "artificial sea water" of "A" alone, or of cystine which has been found capable of replacing it (p. 504), would not allow a vigorous growth of *Ditylum*. There was some other factor "N" in soil and algal extracts and in natural sea water which was not adsorbed on carbon and which was necessary in addition to "A" for a vigorous growth and considerable crop of *Ditylum*.

The action of the group "N" accessories is complementary to the action of group "A". The increase in growth of *Ditylum* brought about by the addition of "A" and "N" together exceeds the sum of the increases brought about by the addition of each singly; the effect of "A" is enhanced by the presence of "N" and vice versa.

The following experiments are typical.

Ditylum cells were washed in "artificial sea water", and equal volumes of media were inoculated with equal volumes of the *Ditylum* suspension on February 14. On February 28 counts were made with the following result:

Nature of medium	Cells per c.c.
Artificial sea water, enriched N, P and Fe	180
,, ,, +*Fucus* extract*	*circa* 2200
,, ,, +carbon adsorbed fraction†	678
,, ,, +non-adsorbed fraction†	517
,, ,, +carbon adsorbed† and non-adsorbed fractions†	1818

The *Fucus* extract had been broken down by bacteria and dialysed. The quantity * added per litre of artificial sea water was derived from 14 g. of *Fucus*. After fractionating by adsorption on carbon, the quantity of either fraction † added per litre of water was derived from 20 g. of *Fucus*.

The increase of cells per c.c. was

498 due to the addition of the adsorbed fraction,

1301 due to the addition of the adsorbed fraction in the presence of the non-adsorbed fraction.

---

* The extract from 0·5 g. of *Ulva* added to 1 l. of "artificial sea water" was sufficient for the growth of *Thalassiosira*.

In another experiment, carried out in the same manner, the following counts after 8 days' growth (March 15–23) were made:

Nature of medium	Cells per c.c.
Artificial sea water enriched N, P and Fe	70
,, carbon adsorbed fraction from *Fucus* extract	145
,, non-adsorbed fraction from *Fucus* extract	225
,, non-adsorbed + adsorbed fraction	780
,, ,, + adsorbed fraction from "winter" sea water	590
,, ,, + cystine (20 mg./l.)	1600
,, Cystine (20 mg./l.)	330

The increase in number of cells per c.c. was

260 due to the addition of cystine,
1375 due to the addition of cystine in the presence of the non-adsorbed fraction,
75 due to the addition of the adsorbed fraction,
555 due to the addition of the adsorbed fraction in the presence of the non-adsorbed fraction.

The complementary effect of the two fractions was even more marked in several other experiments. Thus in one experiment the increase in number of cells per c.c. was

109 due to addition of cystine alone,
1636 due to addition of cystine alone in presence of non-adsorbed fraction from *Fucus*.

On the Nature of "A" Accessories

Soil extract has been extensively used as a source of "growth stimulant" or "accessory nutrients" in rearing various marine larvae, Protozoa and algae *in vitro*. It appears that its effect is not limited to very simple organisms. Pringsheim, who has reviewed the literature (1936), has found from his own experiments on flagellates that the active principle was adsorbed on carbon and was insoluble in ether and in alcohol.

From experiments on the growth of *Ditylum* in enriched sea water collected during the summer of 1937 it was found that an active principle was adsorbed on carbon from either neutral or acid soil and algal extracts. It could be eluted from the carbon by a solution of ammonia or by boiling with acid alcohol and subsequent treatment with alkali. The addition of this eluted preparation to enriched "summer" sea water rendered it capable of growing a considerable crop of *Ditylum*.

The most convenient method was to boil soil extract, or algal extracts which had undergone bacterial decomposition, or natural sea water, with "decolorizing carbon" which had previously been heated to a dull red and washed with hot hydrochloric acid. The carbon, after washing with water, was then eluted at least twice with a hot 2½ % solution of ammonia in 60 % acetone. The solution was evaporated, dissolved in dilute sodium bicarbonate, dried to get rid of ammonium, and then neutralized.

It was also found that on heating under a reflux with acid alcohol, the active "A" principle passed into solution, presumably as an ester or internal anhydride. On drying and heating with sodium bicarbonate to saponify, active preparations were obtained. The active principle, as Pringsheim had found, was not dissolved in boiling alcohol or ether from either acid, alkaline or neutral residues.

The "ester" after freeing from acid alcohol was sometimes insoluble and sometimes partly soluble in ether. Ether solutions, which were active after saponification, were obtained in some instances, but not always.

It is concluded from these experiments that part at least of the "A" activity is due to an organic acid. The difficulty of obtaining an ether solution of its "ester" suggests that it has either basic properties or many hydroxyl groups.

The concentration of the active principle from extracts of algae presented difficulties, mostly owing to its being readily adsorbed on the impurities when they were precipitated. Continuous extraction with warm aqueous butyl alcohol proved useful, as this removed many of the amino acids and left the "A". To assess the losses which occurred during each step of a process was also impracticable during the earlier steps, since the addition of a crude extract to sea water led to a considerable development of bacteria which sometimes, but not always, interfered materially with the growth of the diatoms.

The proliferation of bacteria in a diatom culture is usual when the diatoms start to die and their soluble organic constituents diffuse into the water, providing food for the bacteria. It has been frequently considered that the growth of bacteria kills the diatoms, and this undoubtedly happens in some cases. In other cases, the growth of bacteria appears to be the effect rather than the cause of the diatoms' death. In many instances it has been noticed that the addition of an algal extract has led to the culture becoming cloudy with bacteria, but, in spite of this, the addition has brought about increased growth of the diatom.

If the addition of a preparation led to little or no increased growth there was always the possibility that, although active, its effect had been offset by the growth of bacteria. Moreover, a falling off in activity has been noticed in many of the preparations, some of which became entirely inactive in the course of a few weeks. The growth of bacteria appears to have little or no destructive effect on active preparations, but the growth of moulds destroys the active principle.

With regard to the quantities of these algal extracts which were necessary to show a well-marked effect on the growth of *Ditylum*, it was found that the extract from 5 g. of *Fucus*, made by boiling with $N/10$ HCl, drying, washing with alcohol and ether and neutralizing, was about the minimum necessary for addition to 1 l. of sterilized "summer" sea water.

Several organic acids, or chemical groups which occur in these acids, are known, which affect the growth of plants and Protozoa, in some cases being *necessary* for the growth of a particular species in artificial media. Hammett (1930) has found that a number of compounds containing divalent sulphur affect the growth of plants and *Paramoecium*; of these substances cystine is typical.

The effect of adding *l*-cystine to water collected during the summer of 1937 was tried and found to give positive results. It brought about a moderate growth provided it was added in relatively large quantity, 10 mg./l. or more. At concentrations of 1 mg./l. or less it had only a slight effect. Later experiments with natural sea waters suggested that 0·5 mg./l., or possibly rather less, may materially increase the growth of this diatom, provided iron, manganese, silica and naturally occurring organic compounds were present in sufficiency.

It is thought that "A" occurring naturally in sea water is unlikely to be cystine only, although this occurs abundantly in marine algae (Mazur & Clark, 1938), and is readily adsorbed on carbon under the conditions employed in this investigation. In the first place the total organic matter in sea water probably does not exceed 5 mg./l. (Keys, Christiensen & Krogh, 1935), and in the second place an active preparation has been obtained by adsorption on carbon from an algal extract which had been deaminated.

Cystine, however, has proved most valuable throughout these experiments as a *substitute for group A*, and, incidentally, for keeping stock cultures healthy and actively dividing.

Glutathione which contains the same $—S.CH_2.CH(NH_2)COOH$ group and methionine $CH_3.S.CH_2.CH(NH_2)COOH$ were found to act in the same way as cystine.

It is known that the addition of aneurin (vitamin B_1) is effective in promoting the growth of various moulds, bacteria and the embryos of higher plants in synthetic media, and that in some cases its immediate degradation products are equally effective.

The effect of adding aneurin chloride in place of "A" accessories was then tried. It was usually found to be active in concentrations down to about 0·25 mg./l.

Growth of *Ditylum* after 10 days (May 13–24) in artificial sea water containing nitrates, phosphates, iron, "additional salts" and N_R (see p. 507):

	Cells per c.c.
With no further addition	526
With 1·25 mg./l. aneurin chloride	1170
With 0·25 " "	1000
With 0·05 " "	700

Again, the concentration of aneurin is much higher than could be expected to have occurred in sea water during the winter of 1938, and, moreover, in several instances it has been found to have no effect.

Another pure substance, the supply of which affects the growths of higher plants, yeasts and moulds, is biotin, the bios II of yeast, a basic sulphur containing acid, isolated from the yolk of eggs by Kögl & Tonnis (1936) after a long series of fractionations which included adsorption on carbon and "esterification". Starting from an extract of egg yolks and following the earlier stages of fractionation (precipitation of impurities with 50 % acetone, 85 % alcohol, normal and basic lead acetate, followed by adsorption on carbon), a crude preparation was made of which the biotin content was calculated from Kögl & Tonnis's data. This was found to be active, replacing "A", in experiments with *Ditylum* in artificial sea water. Provided that its activity was due entirely to its biotin content and not to impurities, the concentration necessary was of the order of 0·005–0·01 mg. biotin per litre.

This is more nearly approaching a concentration which might conceivably occur in the sea; moreover, the active principle in algal extracts behaves like biotin in so far as its properties have been observed.

It has been found by Kögl & Haagen-Smit (1936) that aneurin and biotin together had more effect on the growth of pea embryos in synthetic media than the effect of each singly. Kögl & Fries (1937) have found that some moulds require aneurin while others need biotin also for growth in synthetic media. With this in view, the effect of a mixture of 0·002 mg. aneurin and 0·0005 mg. "biotin" per litre was tried in place of "A", but found inactive towards the growth of *Ditylum* at these dilutions.

These experiments show that "A" activity is not limited to a single compound, and lend support to the idea that "A" occurring naturally in sea water may be a group of substances. It is perhaps significant that both aneurin, biotin, cystine and the related compounds glutathione and methionene all contain divalent sulphur.

ON "N" ACCESSORIES OCCURRING IN ALGAL EXTRACTS

The crude preparations of "N", left after adsorbing the "A" content on carbon from algal or soil extracts, would naturally contain traces of various elements which may be beneficent or necessary for the growth of *Ditylum* and may be absent in this artificial sea water. Boron, which is present to the extent of some 5 mg./l., is an instance, none having been included in the artificial sea water.

It was found that the addition of borate did cause improved growth of *Ditylum*, and the further addition, to the extent of 0·025 mg./l., of copper, manganous, arsenic as arsenate, cobalt and zinc salts caused an even slightly better growth. It is seen from the following experiment that these "additional salts" did not take the place of "N".

Equal quantities of *Ditylum* were used to inseminate equal volumes of artificial sea water enriched with nitrates, phosphates and iron. After 7 days' growth (March 25–April 1) the following populations were found:

	Cells per c.c.
In artificial sea water	46
” ” +cystine 20 mg./l.	160
” ” +cystine+"additional salts"	315
” ” +cystine+non-adsorbed fraction of *Fucus* extract	1190

The further addition of iodate, iodide and bromide was without apparent effect.

Experiments with non-adsorbed fractions of algal extracts showed that the active "N" principle was insoluble in ethyl and butyl alcohol, in acetone and in ether, but soluble in warm aqueous butyl alcohol. It was destroyed by ashing and by boiling with acid alcohol, suggesting that it is an organic compound.

It was found that treatment with normal aqueous hydrochloric acid at boiling-point, with subsequent evaporation and neutralization, made the fraction more active. It is concluded that part of the "N" occurred in combination in the algal extract and was set free by this treatment. Similar treatment with sodium bicarbonate had little effect on the activity. The extent to which such activation is brought about by evaporating with normal hydrochloric acid is shown in the following experiment:

Equal quantities of *Ditylum* were added to equal volumes of artificial sea water enriched with nitrate, phosphate, iron, "additional elements" and cystine. After 7 and 14 days' growth the number of cells were counted (April 12–26):

	After 7 days	After 14 days
No addition	86	95
+ non-adsorbed fractions of *Fucus* extract	230	1875
+ same treated hydrochloric acid	267	4060

Fractionation of *Fucus* extracts after the "A" had been adsorbed on carbon was attempted. It was found that the active "N" principle was not precipitated by normal lead acetate, but was partly precipitated by basic lead acetate, from which it could be regenerated by the action of sulphuretted hydrogen.

The fraction so obtained, which will be termed "N_R" when added to artificial sea water together with "A" or cystine or aneurin chloride or crude "biotin", allowed a vigorous growth of *Ditylum* to take place with the production of some thousand cells per c.c.

Several preparations of "N_R" have been made from algal extracts which were first treated with normal lead acetate, filtered, and then made alkaline with ammonia; the washed precipitate was suspended in water made acid with HCl, treated with sulphuretted hydrogen for 24 hr. or longer, boiled and filtered clear from lead sulphide. After boiling with carbon the solution was evaporated, dissolved in dilute sodium bicarbonate and again dried to get rid of ammonium. After neutralization, these preparations showed an activity complementary to accessory "A" or cystine.

The growth which occurred in five illustrative experiments is shown in the following table. The experiments were made in the manner already described:

Nature of medium	Cells per c.c. After 7 days
Exp. (April 12–19).	
Artificial sea water	27
„ „ + adsorbed fraction from *Ulva*	25
„ „ + non-adsorbed fraction from *Fucus*	73
„ „ + adsorbed + non-adsorbed fractions	206
„ „ + N_R	34
„ „ + N_R + adsorbed fraction + "additional salts"	150

Exp. (April 25–May 5).	After 7 days	After 10 days
Artificial sea water containing "additional salts"	29	*circa* 29
„ „ + N_R	42	74
„ „ + aneurin chloride 0·25 mg./l.	29	*circa* 29
„ „ + N_R + aneurin chloride	250	320
„ „ + cystine 20 mg./l.	119	156
„ „ + cystine + N_R	590	*circa* 590
*Natural sea water (sample *a*) collected April 1938	461	860
* „ „ (sample *b*) collected January 1938	220	350

* Enriched with nitrate, phosphate and iron to the same degree as the artificial sea water.

Nature of medium	Cells per c.c.
Exp. (May 13–23).	After 10 days
Artificial sea water containing "additional salts"	184
,, ,, $+N_R$	254
,, ,, +cystine 20 mg./l.	456
,, ,, $+N_R$+cystine	1120
Exp. (March 29–April 4).	
Artificial sea water	61
,, ,, $+N_R$	82
,, ,, +cystine 20 mg./l.	170
,, ,, +cystine$+N_R$	645
,, ,, +non-adsorbed fraction from *Fucus*	84
,, ,, +non-adsorbed fraction+cystine	1720
Exp. (April 30–May 9).	After 6 days
Artificial sea water with "additional salts" and with N_R	42
,, ,, +cystine 10 mg./l.	372
,, ,, +biotin 0·01 mg./l. containing "impurities"	277
,, ,, +biotin 0·001 mg./l.	122
* Natural sea water collected January 1938	561

* Enriched with nitrate, phosphate and iron to the same degree as the artificial sea water.

It was particularly noticeable that, in order to obtain a good growth of *Ditylum* in artificial sea water, preparations of "A" and "N" derived from relatively large quantities of algae were required. It is assumed that losses in preparation were great. The additions of an extract of *Fucus*, which had undergone bacterial breakdown and had not been subjected to further fractionation, allowed a considerable growth of *Ditylum* when added in much smaller quantity.

It was observed that preparations of "A" and "N" were liable to lose activity on keeping. Sometimes they lost their activity within a few weeks; in one instance this happened with a preparation which had been kept with its activity apparently unimpaired for several months previously.

The growth of *Ditylum* in artificial sea water with added accessories was rarely so good as in a natural, freshly collected "1937–8 winter" sea water. No general conclusion can be drawn, but it does seem likely that the "A" and "N" in "fertile" sea water are both groups of substances, and that the preparations used in these experiments did not contain all the accessories needed for optimum growth, although they sufficed for a moderate growth owing perhaps to their having been added in large quantity.

These experiments with artificial sea water have indicated that "A" accessories—replaceable by the $\text{—S—CH}_2\text{CH(NH)}_2\text{COOH}$ group—are necessary for the growth of *Ditylum*. They even suggest that, for this species and for the media employed, "A" accessories act as a limiting factor in the sense used by Blackman. An alternative view, perhaps better justified by subsequent experiments is that there are a number of accessory or growth promoting substances, including the potent $\text{S—CH}_2\text{—CH(NH)}_2\text{COOH}$ group, an increase in any one of which *tends* to bring about increased growth, and will do so if other, interacting, substances are present.

CONCERNING THE "PHYSIOLOGICAL STATE" OF THE INOCULUM

When inoculating a series of samples of media to test their relative capacity to support a growth of *Ditylum*, actively dividing cells from a stock culture were always used. Excellent agreement between their growth in duplicate samples was obtained. On repeating the experiments, using actively dividing cells, usually from a subculture of the stock previously used, similar results were usually obtained. In the repeat experiments conditions for growth were not *identical* with the conditions in the previous experiment. In particular, the illumination differed during the course of the two experiments. Occasionally it happened that the repeat experiments did not show the beneficial effects of an added accessory which were shown in the previous experiment; this happened several times when using vitamin B_1 in place of "A".

It was apparent that the response of the inoculum to the conditions of the experiment—light, quantities and nature of the "A" and "N" accessories added, temperature, etc.—depended to some extent on the "physiological state" of the *Ditylum* cells in the inoculum. For instance, it was noticed that insemination with very rapidly dividing cells, such as occurred in a stock culture during bright weather at 13°, tended to give a greater crop than an insemination with less rapidly dividing cells, as from a stock culture at 8°, or one at 13° in which a considerable growth had already taken place, the growth rate had started to slow down and the cells had become darker in colour than during the earlier and more rapidly growing phase.

The optimum conditions of light, for growth of a diatom, appear to depend to a large extent upon the conditions under which the diatom has lived previously, that is upon its "physiological state". This is illustrated in the following experiment:

A culture of *Biddulphia mobiliensis* was divided into two parts. One was then grown in a north window in relatively dim December light. The other portion was grown near an electric bulb immersed in a bowl of running water; it received continuous light of some 18,000 lux. The illumination was measured with a photometer which Dr W. R. G. Atkins had very kindly rated for me in diffuse daylight of varying intensities against a similar photometer which had been standardized in artificial mean noon sunlight. At the end of a week, subcultures of each of these cultures were made in sea water enriched to the same extent. Each subculture was divided into ten glass vessels. They were immersed in two water-baths, one kept at 13° C., the other at 18° C., at different distances from an electric bulb which was immersed in each bath. The light which each vessel of culture received was measured. After 72 hr. continuous light, a sample from each vessel was taken out, poisoned, and the diatoms per c.c. counted. From these counts the percentage increase in number of cells which had taken place during the 72 hr. was calculated:

	Temp.	Percentage increase in 72 hr. at				
	° C.	28,000	18,000	8000	4100	1400 lux
Cells grown previously in dim light	18°	7	68	66	106	87 %
	13°	24	16	14	8	2 %
Cells grown previously in continuous light at 18,000 lux	18°	171	236	190	123	98 %
	13°	31	70	105	67	36 %

This experiment is interpreted as showing that the optimum light intensity varies both with the "physiological state" of the diatom and with the temperature, and, furthermore, that the effect of temperature on growth rate varies with both the light intensity and the physiological state of the diatom.

In view of this experiment it is not surprising that similar results were not invariably obtained in experiments carried out at different illuminations and with inseminations of *Ditylum* which had lived under different conditions. In these experiments the nature and quantity of the added substances were controlled, but the other two variables—"physiological state" of the inoculum and light intensity—were not controlled. Moreover, it is possible that differences in the "physiological state" of the diatom are bound up with differences in its capacity to synthesize factors which it requires for vigorous growth, or to utilize partly preformed substances in the external medium for the final production of its requirements. Thus it has been found for some species of bacteria, that they lose their power of growing in synthetic media if they have been cultured persistently in a medium containing a preformed "factor".

Some observations made in particularly dull weather during the winter of 1938 suggest that, for slow growth, the requirements of *Ditylum* are different from its requirements for rapid growth during bright weather. It was noticed that the response to addition of organic compounds having "N" activity was less than during bright weather.

Growth in Natural Sea Water

When actively growing cells of *Ditylum* were transferred to natural sea water, collected several miles offshore at intervals during the summer of 1937 and enriched with nitrate phosphate and iron citrate, they ceased making vegetative divisions and many of the cells formed auxospores which did not develop. In water collected in late October 1937, enriched in the same way, the cells continued vegetative growth, and this ability of the water to support vegetative growth was found in samples collected at intervals during the winter and following spring, mostly at a distance of 20 miles offshore. By June 1938 there was a falling off in the growth which the water would support after enrichment.

Water collected from the surface on July 12, filtered and enriched, allowed only a few divisions to take place. Water collected on July 24 from 5, 15 and 50 m. at a position 20 miles offshore would allow no more than some two divisions to take place before either auxospores developed or the cells died.

On July 28 water samples collected on July 12 and 24 were filtered, sterilized and enriched with N, P and Fe in identical manner, they were inseminated with 21 cells of *Ditylum* (strain T) per c.c. On August 2 counts were made:

	Vegetative cells	Auxospores
Surface water of July 12	268	55 per c.c.
From 15 m. July 24	4	65
„ 5 „ „	Similar to 15 m.	
„ 50 „ „	Similar to 15 m.	

On July 29 a similar experiment was made using strain G *Ditylum* of which 19 cells per c.c. were added. On August 3 counts were made:

	Vegetative cells	Auxospores
Surface water of July 12	106	38 per c.c.
From 15 m. July 24	10	30

These waters collected in July 1938 behaved towards *Ditylum* in the same way as waters collected at intervals during the summer of the previous year.

The July waters responded to the addition of cystine alone, allowing a healthy growth and moderate crop of *Ditylum*, with the exception of water from 15 m. collected on July 24. This sample only gave a poor growth with the addition of cystine, but with the further addition of an *Ulva* preparation containing "N" it behaved as the others did with the addition of cystine only, giving a healthy and vigorous growth.

In the course of experiments on the growth of *Thalassiosira gravida* in artificial sea water Allen (1914) had observed that the addition of a small percentage of sea water from the aquarium tanks was more effective in promoting a vigorous growth of the diatom than similar additions of water collected from the sea. "The tanks of the Plymouth Aquarium are worked on a closed system of circulation, the same sea water being circulated over and over again, so that the principal difference between the water taken from them and that obtained from outside consists in the greater abundance in the tank water of organic compounds, which result from the metabolism of living organisms." He further observed that "on the whole, samples of water taken from Plymouth Sound give better growths than are obtained from samples from the English Channel in the neighbourhood of the Eddystone". The water in Plymouth Sound contains more organic matter in solution than water from the open sea. It receives a continuous discharge of sewage in addition to land drainage.

On August 12 samples of water were collected from

(*a*) The entrance to Plymouth Sound, off Penlee Point, at half ebb from near the surface.

(*b*) A position 6 miles offshore from near the surface.

(*c*) A position 20 miles offshore from near the surface.

(*d*) A position 20 miles offshore from 5 m. depth.

(*e*) A position 20 miles offshore from 50 m. depth.

Each sample was filtered, heated, and enriched with nitrate, phosphate and iron on August 17 in identical manner and inseminated with the same quantity of *Ditylum* cells washed with and suspended in artificial sea water. The cells were of various sizes, some narrow and long, others broad and short which had developed from auxospores about a week previously; the initial population of added cells was 28 per c.c. Two days later auxospores had developed in the waters from 5 and 50 m. depths.

On August 22 counts of the living cells were made:

	Cells per c.c., including auxospores
In water from surface, 20 miles offshore	284, many auxospores
,, ,, 5 m., 20 miles offshore	53, nearly all auxospores
,, ,, 50 m., 20 miles offshore	138, nearly all auxospores
,, ,, surface, 6 miles offshore	238, many auxospores
,, ,, surface, off Penlee Point	1800, no auxospores

As part of this experiment the same series was also grown, with the addition of 10 mg./l. of cystine. The same quantities of the same *Ditylum* were used to inseminate the waters. The same light conditions and temperature prevailed, the cultures being kept on a revolving table. On August 22 counts were made:

	Cells per c.c. including auxospores
In water from surface, 20 miles offshore + cystine	2400, no auxospores
,, ,, 5 m., 20 miles offshore + cystine	437, some auxospores
,, ,, 50 m., 20 miles offshore + cystine	284, nearly all auxospores
,, ,, Surface, 6 miles offshore + cystine	*circa* 2400, no auxospores
,, ,, Surface, off Penlee Point + cystine	2500, no auxospores

Similar results were obtained in further experiments. With the onset of winter of 1938 there was no change in the inability of offshore water to support a vegetative growth of *Ditylum*. Waters collected on November 4 and 29 1938 and January 2 1939 proved singularly infertile after enrichment with nitrate, phosphate and iron.

Meanwhile a series of experiments had shown that lack of manganese in natural sea waters could render them infertile for *Ditylum*. The addition of 20 mg. Mn per cubic metre to the November 4 and 29 waters in both cases made them capable of supporting a considerable, yet limited, growth of *Ditylum*, some 2000 cells per c.c. being produced.

Offshore sea water collected on November 29 1938 and on January 2 1939 were filtered, heated to 90° C. and enriched with N, P and Fe in identical manner on January 6, when both were inseminated with 26 cells of *Ditylum* per c.c. Additions of cystine and manganese were made and the cultures kept at 13° C. in glass vessels resting on a mirror below a skylight in order to increase illumination. Counts were made at intervals with the following result:

	Cells per c.c. after				
	3 days	5 days	9 days	13 days	22 days
January 2, water:					
No further addition	40	38*a*	*d*	..	..
No further addition	37	26*a*	*d*	..	..
+5 mg./l. cystine	62	66	*d*	..	..
+2 mg./m.^{3} manganese	59	85	223*a*	428*a*	..
+10 mg./m.^{3} manganese	62	100	540	1110	2420
November 29, water:					
No further addition	43	40*a*	*d*	..	..
No further addition	33	33*a*	*d*	..	..
+5 mg./l. cystine	40	35	*d*	..	..
+10 mg./m.^{3} manganese	72	129	613	1560	1950
+10 mg./m.^{3} manganese, 0·25 mg./l. cystine	86	156	860	2130	2150
+10 mg./m.^{3} manganese, 1 mg./l. cystine	79	180	920	2040	2540

a denotes presence of auxospores. *d* denotes disintegrating cells.

With the freshly collected January water, adding a considerable dose of cystine prevented auxospore formation but had little effect on growth. Adding manganese, on the other hand, had a marked effect on growth.

With the water collected on November 29, cystine alone had no effect on growth but prevented auxospore formation. In the presence of an ample sufficiency of manganese, the effect of added cystine became apparent even at a concentration of 0·25 mg./l.

The water collected on January 2 only made a poor growth with the addition of 2 mg. Mn/m.^{3}, so an experiment was made to find out whether the effect of small additions of manganese was considerably augmented by small additions of cystine. It showed that the addition of 0·5 mg. Mn/m.^{3} had little effect and the addition to this of 0·5 mg. cystine per litre brought about only a slight further increase. This small quantity of cystine caused only a small increase to the growth brought about by the addition of 2 mg. Mn/m.^{3} when added in conjunction with it.

Effect of Storage on Natural Sea Water

A quantity of offshore sea water collected in January 1938 was filtered and, after enrichment with nitrates, phosphates and iron, found able to support a healthy growth of *Ditylum* yielding a moderate crop. Unfortunately no counts were made of the final crops these "fertile 1937–8 winter waters" would yield—it is assessed as some 2000 cells of mixed diameters per c.c.

After being stored in a glass vessel for several months, it was noticed that this water would no longer support a good growth. By the end of July it would only allow a few cell divisions to take place. The growth was not greatly increased by the addition of cystine, nor was it increased by keeping the culture cool and in a dim light approaching more closely the physical conditions earlier in the year.

The effect of adding an extract of *Ulva*, from which the "A" active substances had been adsorbed on carbon, was tried. The addition of this alone did not lead to a vigorous growth such as occurred when both this and cystine were added together.

A carboy of open sea water had been collected in December 1937 and stored, unfiltered. When this was examined in September, after nine months' storage, it was found to behave in the same way as the water stored after filtration in a flask. After enrichment with nitrates, phosphates, and iron and insemination with the diatoms, these made at most one or two vegetative divisions before forming auxospores, which did not develop. The addition of cystine alone brought about a very slight increase in vegetative growth before auxospore formation set in. The addition of yeast extract which had been freed from "A" by continuous extraction with butyl alcohol had almost no effect. The addition of both cystine and extract caused a healthy and vigorous vegetative growth—approximately 1600 cells per c.c. being produced.

ON THE NATURE OF ORGANIC "N" ACCESSORIES

Some information concerning the nature of "A" accessories had been obtained from the experiments with artificial sea water, but virtually no information concerning the "N" group except that an organic substance or substances were probably a necessary part. The next step was clearly to investigate the "N" substances lacking in stored sea water. As a preliminary a number of physiologically active compounds, including heteroauxin, vitamins B_2 and C, β-alanine and nicotinic acid, were tried out for "N" activity without result. Having arrived at this impasse, the following line of reasoning provided the first clue:

(i) A very active preparation of "N" had been obtained by continuous extraction of a yeast extract with (aqueous) butyl alcohol, a process which carries over many of the amino acids.

(ii) It had been noticed that a heavy dosage with cystine of artificial sea water would allow a certain but limited amount of growth by the diatom. This suggested that the $—CH_2—CH(NH_2)COOH$ grouping in cystine itself had a small measure of "N" activity. With this possibility in view the effect of *dl*-α-amino-propionic acid (α-alanine) was tried as a substitute for "N".

When added in concentrations between 1 and 10 mg./l. to stored sea water enriched with nitrates, phosphates, iron, cystine and in some cases manganese, it brought about an increased growth of the diatom in twelve experiments, and no increase in one experiment. Moreover, the effect was complementary to that of cystine in the two following experiments:

Sea water collected January, filtered and stored, enriched with N, P, Fe and inseminated with *Ditylum* September 2 1938. Counts made September 8:

	Cells per c.c.
No further addition	211
10 mg./l. cystine	616
10 mg./l. *dl*-α-alanine	459
10 mg./l. cystine + 10 mg./l. α-alanine	1800

Similar procedure; inseminated September 5, counts made September 10:

	Cells per c.c.
No further addition	135
5 mg./l. cystine	510
5 mg./l. *dl*-α-alanine	266
5 mg./l. *dl*-α-alanine + 5 mg./l. cystine	1450
1 mg./l. *dl*-α-alanine + 5 mg./l. cystine	1250

It is noteworthy that the addition of α-alanine alone had little effect. Subsequent experiments suggested the possibility that the activity of α-alanine and other organic substances might conceivably be due to traces of impurity, such as manganese, but the relative inactivity of these organic substances when added alone without cystine is opposed to this possibility.

Experiments with this and other substances to find whether their addition caused growth in stored sea water enriched with cystine are summarized in the following table, and show that a number of related amino acids do not share the activity of α-alanine.

The effect of adding lactate, in which the amino group occurring in α alanine is replaced by a hydroxyl group, was tried and this was found to be active. Its activity is shared by a number of hydroxy compounds as shown in the table. It may be significant that these hydroxy compounds share the property of forming complexes with iron and with manganese, rendering both metals less readily precipitated in alkaline media. Thus gluconic acid forms complexes with the salts of both metals which are not precipitated in *N*/2 sodium hydroxide.

	Increased growth	No increased growth
dl-$CH_3CH(NH_2)COOH$ *dl*-α-alanine	In 12 exp.	In 1 exp.
d-$CH_3CH(NH_2)COOH$ *d*-α-alanine	1 ,,	3 ,,
$CH_2(NH_2)CH_2COOH$ β-alanine	0 ,,	2 ,,
CH_3CH_2COOH propionic acid	0 ,,	2 ,,
dl-$CH_3CH(OH)COOH$ *dl*-lactic acid	2 ,,	0 ,,
$CH_2(OH)COOH$ glycollic acid	0 ,,	2 ,,
$CH_2(NH_2)COOH$ glycine	Slight in 2 exp.	1 ,,
$CH_3COCOOH$ pyruvic acid	1 exp.	1 ,,
l-$(CH_3)_2.CH.CH_2.CH(NH_2)COOH$ *l*-leucine	Slight in 1 exp.	1 ,,
d-$(CH_3)_2.CH.CH_2.CH(NH_2)COOH$ *d*-leucine	0 exp.	1 ,,
$C_8H_6NCH_2CH(NH_2)COOH$ *l*-tryptophane	0 ,,	3 ,,
dl-proline	0 ,,	2 ,,
$C_5H_6(OH)_5COOH$ gluconic acid	5 ,,	3 ,,
d-$C_5H_6(OH)_5CHO$ dextrose	9 ,,	0 ,,
l-$C_5H_6(OH)_5CHO$ laevulose	1 ,,	Doubtful in 1 exp.
$C_6H_6(OH)_6$ inosite	Slight in 3 exp.	1 exp.

In the majority of experiments the quantity added was 2 mg./l., and in many of the experiments the increased growth took place in the presence of added manganese.

It was noticed that the effect of α-alanine appeared less marked as the days became shorter and the diatoms were growing less rapidly. The experiments made in early September with water collected during the previous January were repeated during a period of dull weather starting on November 4 when the samples were inseminated with *Ditylum*. Counts were made on November 7, 9 and 12, when many cells had disintegrated.

	Cells per c.c.		
	Nov. 7	Nov. 9	Nov. 12
January water enriched N, P, Fe	94	66	38
Ditto + 2 mg./l. α-alanine	103	78	39
Ditto + 5 mg./l. cystine	207	420	200
Ditto + 5 mg./l. cystine + 2 mg./l. α-alanine	303	545	460
Ditto + 5 mg./l. + 2 mg./l. dextrose	1040	..	1300

This experiment shows the greater "N" activity of dextrose and bears out the general observation that the effect of α-alanine was less during slow growth in dull weather.

EFFECT OF MANGANESE

In these experiments with organic compounds possessing N activity the final growth or crop was not a large one. It was clear that further growth was held back through lack of some further accessory nutrient.

During the course of the earlier work it had been found that growth in artificial sea water was increased by adding 25 mg./m.^{3} of Cu, Mn, Co, Zn and As as salts. The effect of this same mixture of "additional salts" was tried on growth in stored sea water enriched with N, P, Fe, cystine and α-alanine. It brought about a very markedly increased crop. The following experiment shows that the effect is due, for the most part, to the manganese.

Stored sea water enriched with N, P, Fe, 5 mg./l. cystine and 1 mg./l. α-alanine was inseminated with *Ditylum* in October 5. On October 11 the following observations were made:

In the water as above with no further addition	Almost all auxospores
With 5 mg./m.^{3} Cu, Co and Zn	Slight increase about 50 % auxospores
,, ,, Cu, Zn	
,, ,, Mn, Cu, Co, Zn, As	Heavy growth, no auxospores
,, ,, Mn, Co, Zn	
,, ,, Mn, Cu, Zn	
,, ,, Mn, Cu, Co	
,, ,, Mn, Cu, Co, Zn	
,, ,, Mn, Cu	

It appeared from these and subsequent experiments that a very small supply of *manganese promotes continued growth* of this *Ditylum*.

The amount of manganese in samples of ocean and inshore waters from various depths has been estimated by Thompson and Wilson (1935), who found quantities varying between 1 and 10 mg./m.^{3}

Continued experiments with stored sea water showed that after enrichment with N, P and Fe, the addition of 10 to 20 mg./m.^{3} of manganese would allow a moderate, and sometimes good, growth of *Ditylum*. Furthermore, offshore water collected on November 4 1938 which after filtering, sterilizing and enrichment with N, P and Fe, allowed no growth of the *Ditylum*, behaving like stored water, on adding 10 mg./m.^{3} of manganese permitted a good growth to take place. Waters collected on November 28 1938, and January 2 1939 behaved in the same manner.

When cystine and one of the "N"-active organic compounds, as gluconic acid or dextrose, was added to the enriched stored sea water in addition to manganese, still further increased crops were obtained. A number of experiments were made, with such additions and it became apparent that growth was finally brought to a standstill through lack of another necessary substance. The water, amply enriched with N and P and, as far as one could judge, with Fe, Mn and organic compounds, having A and N activity, would not allow more than some five or six thousand cells per c.c. to develop. When such numbers were approached the cells became misshapen and had the general appearance of diatoms lacking silica.

A dilute solution of commercial waterglass was neutralized with hydrochloric acid to give a sol containing *ca.* 0·1 % of SiO_2. On adding this to provide some 20 mg. SiO_2/l. to stored sea water enriched with N, P, Fe, Mn, cystine and gluconic acid, a growth exceeding 20,000 cells per c.c. was obtained, turning the medium the colour of pale sherry. It was found that without the cystine and gluconic acid a very considerable growth would take place provided manganese and silica were added. It appeared either that the commercial water glass contained (? organic) accessory substances or that the stored sea water contained sufficient to allow a very heavy growth in the presence of ample SiO_2 and Mn. Neutral silica sols were therefore made from the same sample of waterglass after it had been dried and heated to bright redness in a platinum crucible and also from silicon tetrachloride. The growth induced by adding these was less rapid than the growth induced by adding the sol made from (unheated) waterglass, but the final growth in all three cases was similar. A reagent blank containing the sodium hydroxide and hydrochloric acid used in making the sol from silicon tetrachloride was included in the experiment.

Stored sea water enriched with N, P, Fe and 0·02 mg. Mn/l., inseminated November 4. Counts made November 14 and 21.

	Nov. 14 cells per c.c.	Nov. 21
No further addition	1210	*circa* 2700
With reagent blank	1240	” ”
With 20 mg. SiO_2/l.		
ex commercial waterglass	3440	*circa* 15,000
ex commercial waterglass (heated)	1860	” ”
ex $SiCl_4$	1860	” ”

Thus it appears that commercial waterglass contains some substance other than silica which increases the diatoms growth rate, and that this substance is destroyed or rendered inactive by heating to redness.

This and a number of subsequent experiments all showed that the stored natural sea water would support a growth when manganese and silica were added, without any addition of organic accessories other than the citrate added with the iron. The further addition of reasonably small quantities of cystine, 1–2 mg./l., led to heavier crops.

Experiments were made to find the quantity of manganese required to allow a continued and vigorous growth of *Ditylum* in stored sea water in the presence of other accessories added in ample quantity, i.e. silica, cystine, iron and gluconic acid. These indicate that 1–2 mg./m.^{3} of manganese is sufficient, while greater concentrations cause more rapid growth, but not necessarily greater crops.

Exp. (Dec. 2–9).

	Cells per c.c.	
	Dec. 6	Dec. 9
No manganese added	75	*circa* 75
2 mg./m.^{3} manganese added	1900	*circa* 7000
5 mg./m.^{3} manganese added	2740	7000
10 mg./m.^{3} manganese added	3500	7000

Exp. Dec 14–29.

	Cells per c.c. Dec. 29
No manganese added	175
0·5 mg./m.^{3}	1400
1·0 mg./m.^{3}	2000

THE EFFECT OF OTHER INORGANIC SALTS

The experiments with stored sea water had amply shown that it would support a luxuriant growth resulting in an exceptionally heavy crop of the diatom if there were added nitrate, phosphate, silicate, iron as a complex with a polyhydroxy organic compound, manganese and the $—S—CH_2CH(NH_2)COOH$ group. Later, in 1939, it was found that such additions would no longer allow such heavy crops, due, apparently, to the long periods of very dull weather or to a further change in the stored water. Alanine and dextrose when added in addition had little effect in promoting greater crops, although both these substances had a marked effect when added to the same water enriched in the same way, but without added silicate during the previous September and November. Meanwhile, experiments made with artificial sea water had suggested that other elements occurring in minute traces in the water may play some part in the diatoms' metabolism. With this possibility in view the effect of adding such "trace elements" to the stored sea water in addition to iron, manganese and cystine was tried. A preparation containing a representative mixture of such elements likely to play a part in plant metabolism was made by boiling coal ash with hydrochloric acid, evaporating, redissolving and neutralizing to *p*H 7. In three experiments this was found to have a marked effect in increasing the diatoms' growth.

I have great pleasure in acknowledging the many helpful suggestions I have received during the course of this investigation, particularly those from Dr L. H. N. Cooper, Dr W. R. G. Atkins, F.R.S. and Dr E. J. Allen, F.R.S.

SUMMARY

The diatom *Ditylum brightwelli* requires, for vigorous growth in artificial sea water, two organic substances, or groups of substances, in addition to inorganic salts.

The substances, or groups, act in a manner complementary to each other.

The effect of adding either is greatly increased by the presence of the other.

One accessory substance, or group, has been obtained in impure state from natural sea water and from extracts of algae by adsorption on carbon and elution. It has properties of an inorganic acid or internal anhydride. Several organic compounds containing sulphur possess similar activity, including compounds containing the $\text{—S—CH}_2\text{—CH(NH}_2\text{)COOH}$ group.

The other substance or group has been obtained in impure state from extracts of algae and of yeast. A number of organic compounds have been found to possess similar activity.

The diatom required manganese, a concentration of one part per thousand million being sufficient for vigorous growth.

The diatom made good growth when transferred to natural sea water, enriched with nitrate, phosphate and iron, collected from offshore at intervals between October 1937 and June 1938.

The diatom ceased growth and formed auxospores when transferred to natural sea water, enriched in the same manner, collected from offshore during the summer of 1937 and during the period between July 1938 and January 1939.

These natural sea waters could be rendered fertile in some cases by adding a compound containing the $\text{—S—CH}_2\text{CH(NH}_2\text{)COOH}$ group and in some cases by adding 1–2 mg. Mn/m.^3

Water collected during the winter of 1938 became infertile after nine months storage, due to loss of available manganese.

REFERENCES

ALLEN, E. J., 1914. On the culture of the plankton diatom *Thalassiosira gravida* Cleve in artificial sea water. *Journ. Mar. Biol. Assoc.*, Vol. x, pp. 417–39.

ALLEN, E. J. & NELSON, E. W., 1910. On the artificial culture of marine plankton organisms. *Quart. Journ. Micr. Sci.*, Vol. 60, pp. 361–431.

GROSS, F., 1937*a*. Life history of some marine plankton diatoms. *Phil. Trans. Roy. Soc.*, B, Vol. 228, pp. 1–47.

GROSS, F., 1937*b*. Notes on the culture of some marine plankton organisms. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 756–68.

HAMMETT, F. S., 1930. The chemical stimulus essential for growth by increase in cell numbers. *Protoplasma*, Vol. 7, pp. 297–322.

HARVEY, H. W., 1933. On the rate of diatom growth. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 253–76.

HARVEY, H. W., 1937. The supply of iron to diatoms. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 205–19.

KEYS, A., CHRISTIENSEN, E. H. & KROGH, A. The organic metabolism of sea water. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 628–46.

KÖGL, F. & FRIES, N., 1937. Ueber den Einfluss von Biotin, Aneurin und Mesoinosit auf das Wachstum verschiedener Pilzarten. *Zeit. phys. Chem.*, Bd. 249, p. 93.

KÖGL, F. & HAAGEN-SMIT, A. J., 1936. Biotin und Aneurin als Phytohormone. *Zeit. physiol. Chem.*, Vol. 243, p. 209.

Kögl, F. & Tonnis, B., 1936. Ueber das Bios Problem. *Zeit. physiol. Chem.*, Vol. 242, p. 43.

Mazur, A. & Clark, H. T., 1938. The amino acids of certain marine algae. *Journ. Biol. Chem.*, Vol. 123, pp. 729–40.

Peach, E. A. & Drummond, J. C., 1924. On the culture of the marine diatom *Nitzschia closterium* f. *minutissima* in artificial sea water. *Biochem. Journ.*, Vol. 18, pp. 464–8.

Pringsheim, E. G., 1936. Der Rätsel der Erdabkochung. *Bot. Centralblatt*, Beiheft 55*a*.

Thompson, T. G. & Wilson, T. L., 1935. The occurrence and determination of manganese in sea water. *Journ. Amer. Chem. Soc.*, Vol. 57, p. 233.

THE BIOLOGY OF *CHTHAMALUS STELLATUS* (POLI)

By Hilary B. Moore, Ph.D.
Biological Station, Bermuda

and J. A. Kitching, M.A., Ph.D.
University Department of Zoology, Bristol

(Text-figs. 1–4)

INTRODUCTION

Chthamalus stellatus (Poli) is a littoral barnacle, very similar both in habitat and in external appearance to another shore barnacle, *Balanus balanoides*. Actually with practice the two species can nearly always be distinguished *in situ* on the rocks (see Moore, 1936, p. 704). Although these two species appear to occupy similar ecological niches on the shore, their geographical distributions are different, since *Chthamalus* replaces *Balanus balanoides* progressively towards the south and west of the British Isles, and eastwards in the English Channel. In this paper an attempt is made to bring together what is known of the biology of *Chthamalus stellatus*, and to make a comparison between this species and *Balanus balanoides*.

MATERIAL AND METHODS

The observations reported in this paper are of very scattered origin, and concern the geographical distribution, relationships with other organisms, and growth rate of the barnacle *Chthamalus stellatus*.

For the investigation of the geographical distribution of *Chthamalus*, records of its presence or absence around the coasts of the British Isles were made by both authors, and also by a number of people who kindly sent material for examination. Except when observers were familiar with the differences between *Chthamalus* and *Balanus balanoides*, such material was always examined personally by one of the authors, and no records of absence were accepted from doubtful sources. The results of this collection of data are described and discussed on pp. 527–31, and summarized in Table I.

Notes on the general relationships of *Chthamalus*, and counts of its density, were made both on the Dorset coast and in the neighbourhood of Loch Sween by J. A. Kitching. Corresponding observations were made in Devon and Cornwall and in the north and west of Scotland by H. B. Moore, with the assistance, in Scotland, of Mr G. M. Spooner. The methods of counting and

TABLE I

Locality no. (see map)	Name of locality	Abundance of *Chthamalus*	Observer, or reference to previous record	Date of field observations
1	Nybster, Caithness	Only 2 found in 15 min. search; *Chthamalus* confined to extreme top of barnacle zone	H. B. Moore	28. vi. 36
2	Dunnet Hd., Caithness	Only 6 seen in 10 min. search; *Chthamalus* confined to top 20 cm. of barnacle zone	H. B. Moore	27. vi. 36
3	Skullomie, Sutherland	Up to 120 per m.^{2}; confined to top 50 cm. of barnacle zone	H. B. Moore	27. vi. 36
4	Geodha Chobhair, Sutherland	Up to 2200 per m.^{2}; confined to top 140 cm. (*ca.*) of barnacle zone	H. B. Moore	24. vi. 36
5	Bay of Stoer, Sutherland	Up to 3800 per m.^{2}	H. B. Moore	22. vi. 36
6	Seana Chamas, Ross	Present	H. B. Moore	20. vi. 36
7	Sgòir Beag, Vatternish, Skye	Abundant; occupying 50–100 cm. at top of barnacle zone	H. B. Moore	15. vi. 36
8	Scurrival Point, Barra, Outer Hebrides	Present	*Mrs N. McMillan	13. vii. 37
9	Breivig Bay, Barra, Outer Hebrides	Present	*Mrs N. McMillan	6. vii. 37
10	Òb Allt an Daraich, Skye	Up to 2400 per m.^{2}	H. B. Moore	11. vi. 36
11	Port na Cullaidh, Elgol, Skye	Up to 3200 per m.^{2}	H. B. Moore	18. vi. 36
12	Ardmore Pt., Mull	Plentiful	Kitching (1935)	5. viii. 34
13	Staffa	Plentiful	Kitching (1935)	14. viii. 34
14	Fionphort, Mull	Scarce	Kitching (1935)	6. viii. 34
15	Sound of Mull, near Loch Aline	Scarce	Kitching (1935)	2. viii. 34
16	Loch Buie, Mull	Plentiful	Kitching (1935)	7. viii. 34
17	South end of Kerrera, Firth of Lorne	Scarce	Kitching (1935)	1. viii. 34
18	Ardnoe Pt., near Crinan	Rather sparse	Kitching (1935)	24. vi. 34
19	Mouth of West Loch Tarbert, Jura	Rather sparse	J. A. Kitching	26. viii. 36
20	Farland Pt., Cumbrae	Up to 480 per m.^{2}	H. B. Moore	5. vii. 35
21	Whiting Bay, Arran	A very few present	H. B. Moore	10. vii. 35
22	Macrihanish, Kintyre	Scarce	Kitching (1935)	27. viii. 34
23	Mull of Kintyre	Absent	Kitching (1935)	27. viii. 34
24	Port Stewart, Co. Londonderry	Present	*Mrs N. McMillan	26. ix. 36
25	Saltpan Rock, 1–2 miles south of Moville, Co. Donegal	Present	*Mrs N. McMillan	28. iii. 37
26	Malin Hd., Co. Donegal	Present	*Mrs N. McMillan	29. iii. 37
27	Horn Hd., Co. Donegal	Present	†Dr J. W. S. Pringle	—. viii. 36
28	Bundoran, Co. Donegal	Present	*Dr R. Lloyd Praeger	8. v. 37
29	Achill I. (west corner), Co. Mayo	Abundant; no *Balanus balanoides* present	Mr D. A. Webb	—. vii. 37
30	Achillbeg I., Co. Mayo	Abundant; about equal in numbers with *B. balanoides*	Mr D. A. Webb	—. vii. 37
31	Dukes, Dingle Bay, Co. Kerry	Present	Dr W. R. G. Atkins	—. ix. 36
32	Rossbehy, Dingle Bay, Co. Kerry	Fairly plentiful	J. A. Kitching	21. vii. 38
33	Castlecove, Co. Kerry	Abundant	*Dr S. Kemp	24. viii. 36
34	Dunmanus Bay, Co. Cork	Abundant	Miss E. M. Moore	—. viii. 36
35	Barley Cove, Co. Cork	Abundant	Miss E. M. Moore	—. viii. 36
36	Middle Calf I., Schull, Co. Cork	Present	*Miss E. M. Moore	24. viii. 36
37	Castle I., Schull, Co. Cork	Present	*Miss E. M. Moore	24. viii. 36
38	Lough Ine, Co. Cork	Present	*Miss E. M. Moore	—. viii. 36
39	Oysterhaven, Co. Cork	Abundant	H. B. Moore	10. vii. 37
40	Fountainstown, Co. Cork	Abundant	H. B. Moore	15. vii. 37
41	Ardmore, Co. Waterford	Abundant	H. B. Moore	8. vii. 37
42	Stradbally, Co. Waterford	Abundant	H. B. Moore	8. vii. 37
43	Greenore Pt., Co. Wexford	Abundant	J. A. Kitching	1. vii. 38
44	Wicklow, Co. Wicklow	Only 2 seen in about 10 m. of shore	H. B. Moore	6. vii. 37
45	Bray Hd., Co. Wicklow	Present; less than 1 per m.^{2}	H. B. Moore	6. vii. 37
46	Ireland's Eye, Co. Dublin	Sparse; only on most wave-beaten rocks	J. A. Kitching	25. vii. 38
47	Greenisland, Co. Antrim	Absent	Mrs N. McMillan	—. viii. 36
48	White Hd., Co. Antrim	Absent	Mrs N. McMillan	—. xii. 36
49	Island Magee, Co. Antrim	Absent	Mrs N. McMillan	29. ix. 36
50	Kirk Michael, I. of Man	Absent	H. B. Moore	—. —. 32
51	‡Port Erin, I. of Man	Absent	H. B. Moore	—. —. 34
52	Langness, I. of Man	Absent	H. B. Moore	—. —. 34
53	Leasowe Embankment, Wirral, Cheshire	Absent	Mrs N. McMillan	18. vi. 37
54	Penrhyn Bay, Llandudno	Absent	Mr D. P. Wilson	3. vii. 35
55	Penmon Pt., Anglesey	Absent	Mr D. P. Wilson	—. ix. 36
56	Bay near Rhosneigr, Anglesey	Absent	Mr D. P. Wilson	—. vii. 37
57	Rhosneigr, Anglesey	Present but very rare	*Mr D. P. Wilson	—. vii. 37
58	Porth Oer, Carnarvon	Present	*Mrs N. McMillan	16. v. 37
59	Bardsey I.	Present	Kidd, Pyefinch & Butler (1935)	—. —. 33

* Specimens examined by H. B. Moore.
† Specimens examined by J. A. Kitching.
‡ An early record by Marrat (1886) is of very doubtful value.

Locality no. (see map)	Name of locality	Abundance of *Chthamalus*	Observer, or reference to previous record	Date of field observations
60	Black Rock, near Criccieth, Carnarvon	Present	*Mrs N. McMillan	16. v. 37
61	Aberystwyth	Present	Walton (1915)	—. —. 15
62	Llangranog, South Cardigan	Present	†Mrs N. McMillan	18. iv. 38
63	Nash Pt., Glamorgan	Plentiful	†Mr G. E. H. Foxon	—. v. 38
64	Clevedon, Somerset	Absent	J. A. Kitching	11. iv. 38
65	Blue Anchor Bay, Somerset	Absent	H. B. Moore	10. xi. 35
66	Lee Bay, North Devon	Abundant	H. B. Moore	31. x. 35
67	Hartland Pt.	Abundant	H. B. Moore	5. viii. 35
68	Millook Haven, North Cornwall	Abundant	H. B. Moore	2. ix. 34
69	Treyarnon	Abundant; up to 70,000 per m.^{2}	H. B. Moore	26. vii. 36
70	Holywell Bay	Abundant	H. B. Moore	26. viii. 36
71	St Ives	Abundant; commoner than *B. balanoides*	H. B. Moore	24. vii. 35
72	Cape Cornwall	Abundant; up to 47,000 per m.^{2}; in very wave-exposed places no *B. balanoides* present	H. B. Moore	6. viii. 36
73	Tresco, Scilly Is.	Abundant	*Mr G. M. Spooner	22. iv. 36
74	Porth Mellin (Mullion Cove)	Abundant	H. B. Moore	28. xii. 35
75	Charlestown, South Cornwall	Abundant	H. B. Moore	28. x. 34
76	Gara Pt., Yealm	Abundant	H. B. Moore	6. iv. 35
77	Black Cove	Abundant	H. B. Moore	21. iv. 35
78	Start Pt.	Abundant	H. B. Moore	21. iv. 35
79	Hope's Nase	Abundant	H. B. Moore	22. iv. 35
80	Dawlish Warren	Abundant	H. B. Moore	31. i. 37
81	Lyme Regis	Fairly abundant	H. B. Moore	21. x. 35
82	Redcliff Pt., Weymouth	Present in a very narrow zone	H. B. Moore	11. i. 36
83	Durlston Pt.	Present	J. A. Kitching	29. vii. 36
84	Old Harry Rocks, near Swanage	Absent	J. A. Kitching	30. vii. 36
85	Freshwater Bay, I. of Wight	Absent	Fischer-Piette (1936)	13. iii. 34
86	St Catherine's Pt., I. of Wight	Absent	Fischer-Piette (1936)	27. ix. 32
87	Culver Cliff, I. of Wight	Absent	Fischer-Piette (1936)	12. iii. 34
88	Newhaven	Absent	Fischer-Piette (1936)	13. v. 33
89	Hythe	Absent	Mr P. R. Crimp	—. ix. 37
90	Dover	Absent	J. A. Kitching	—. iv. 34
91	Flamborough Hd.	Absent	Mr J. H. Fraser	—. x. 36
92	Robin Hood's Bay	Absent	Mr R. Bassindale	—. —. 36
93	Tees Mouth	Absent	Mr R. Bassindale	—. —. 36
94	Bass Rock, Firth of Forth	Absent	H. B. Moore	4. vii. 36
95	Isle of May, Firth of Forth	Absent	J. A. Kitching	8. v. 37
96	St Andrews	Absent	Miss K. M. G. Flemming	—. ii. 38
97	Aberdeen	Absent	Mr A. Milne	—.—. 36
98	Helmsdale, Sutherland	Absent	H. B. Moore	28. vi. 36
99	Bruneval, Normandy	Absent	Fischer-Piette (1932)	6. ii. 31
100	Cap de la Hève	Absent	Fischer-Piette (1932)	30. vi. 27
101	Arromanches	Absent	Fischer-Piette (1932)	7. ii. 32
102	Grandcamp-les-Bains	Absent	Fischer-Piette (1932)	28. vii. 30
103	Pointe de Barfleur	Absent	Fischer-Piette (1932)	31. vii. 27
104	Cap Levi	Absent	Fischer-Piette (1932)	18. vii. 31
105	Cap de la Hague	Absent	Fischer-Piette (1932)	31. vii. 27
106	Flamanville	Absent	Fischer-Piette (1932)	30. iv. 30
107	Carteret	Up to 100 per m.^{2}	Fischer-Piette (1932)	30. iv. 30
108	Ile Lihou, Guernsey	Very few; about 1 per m.^{2}	Fischer-Piette (1932)	30. v. 31
109	La Corbière, Jersey	A very few	Fischer-Piette (1932)	20. iv. 30
110	Saint Germain-sur-Ay	A few	Fischer-Piette (1932)	28. iv. 30
111	Granville	Scarce	Fischer-Piette (1932)	4. ix. 26
112	Cancale, pointe du Grouin	Abundant in upper part of shore	Fischer-Piette (1932)	29. vi. 30
113	Cap Fréhel	Abundant	Fischer-Piette (1932)	12. vii. 32
114	Pointe de Pordic	Abundant	Fischer-Piette (1932)	23. ii. 32
115	Bréhat	Abundant	Fischer-Piette (1932)	21. iv. 32
116	Ploumanach	Abundant in places	Fischer-Piette (1932)	27. ix. 31
117	Ile d'Ouessant	Abundant	Fischer-Piette (1936)	11–15. ii. 33

* Specimens examined by H. B. Moore. † Specimens examined by J. A. Kitching.

of determining the tissue weights of the *Chthamalus* were those already used by Moore (1935, p. 264; 1936, p. 703) in similar work on *Balanus balanoides*.

Finally, observations on the growth rate were made by H. B. Moore on a rock at Drake's Island, Plymouth Sound. For this purpose patches of *Chthamalus* at three different levels were photographed for future recognition, and the individuals were measured *in situ* at intervals. These results are shown graphically in Fig. 4, and discussed on pp. 536–8.

Larval History and Settlement of Spat

Developing larvae were found by Bassindale (1936) in the mantle cavity of *Chthamalus* at Plymouth from July to September. In cultures these larvae reached the sixth naupliar stage in 2–3 weeks, and they would presumably have reached the cypris stage soon after had they lived. Settlement of spat took place at Plymouth during the late autumn and winter. Hatton & Fischer-Piette (1932) have given the first dates of settlement at St Malo in 1931 and 1932 as September 14 and 24 respectively, and according to Hatton (1938) settlement continues for 5 months.

The naupliar stages have been illustrated by Bassindale (1936). The larva is very much smaller than that of *Balanus balanoides*. The sixth stage nauplius has a length of only 0·49 mm., as compared with the 1·15 mm. attained by *Balanus balanoides* at this stage. Also the newly settled young of *Chthamalus* is much smaller than that of *Balanus balanoides*.

The following figures have been given by Hatton (1938), and partly by Hatton & Fischer-Piette (1932), for the population density of *Chthamalus* spat (per 1/100 sq. m.) from counts made in January or February, when settlement was complete:

	High wave exposure		Slight wave exposure	
Level	1931	1932	1931	1932
Just above high water of neap tides	21	21	48	60
Just below high water of neap tides	270	205	39	42
Mid-tide level	1830	1610	8	19
Low water of neap tides	8	5	0	0

They show that the density of settlement was greatest at the highest wave exposure, and suggest also a shift of the optimal level for settlement of the spat from about mid-tide level at the higher wave exposure to high water of neap tides at the more sheltered locality. There was no settlement in a position of extreme shelter (Hatton & Fischer-Piette, 1932).

Zonation, and Interrelations with *BALANUS BALANOIDES*

Lower limit of vertical distribution

For *Chthamalus*, as for *Balanus balanoides*, the lower limit of distribution on the shore is very variable and difficult to determine. However, it may be stated that *Chthamalus* rarely if ever occurs below low water of spring tides. It is hard to see why it should not do so in a favourable situation, since Fischer (1928) has shown that it can survive a continuous immersion of 12 months under natural conditions. It is not possible to say whether it is excluded by some physical factor, such as excessive immersion (see below), or by competition with sublittoral organisms such as coralline algae or other rock-encrusting forms. The adverse factor, whatever it may be, might only operate at some particular stage in the life history of the *Chthamalus*, e.g. on newly attached larvae. It is quite possibly the same factor which prevents *Balanus balanoides* from extending below low water of spring tides.

Actually the lower limit of *Chthamalus* is in many districts far above low water of spring tides, and it may be above high water of neap tides (Fig. 1). No doubt the same factors which locally restrict *Balanus balanoides* also operate against *Chthamalus*—as for instance the rubbing action of the fronds of the larger algae (see Kitching, 1935, p. 363), and competition for space with other sessile organisms such as *Corallina officinalis* (see Moore, 1935, p. 299, for competition of *Balanus balanoides* and *Spirorbis borealis*).

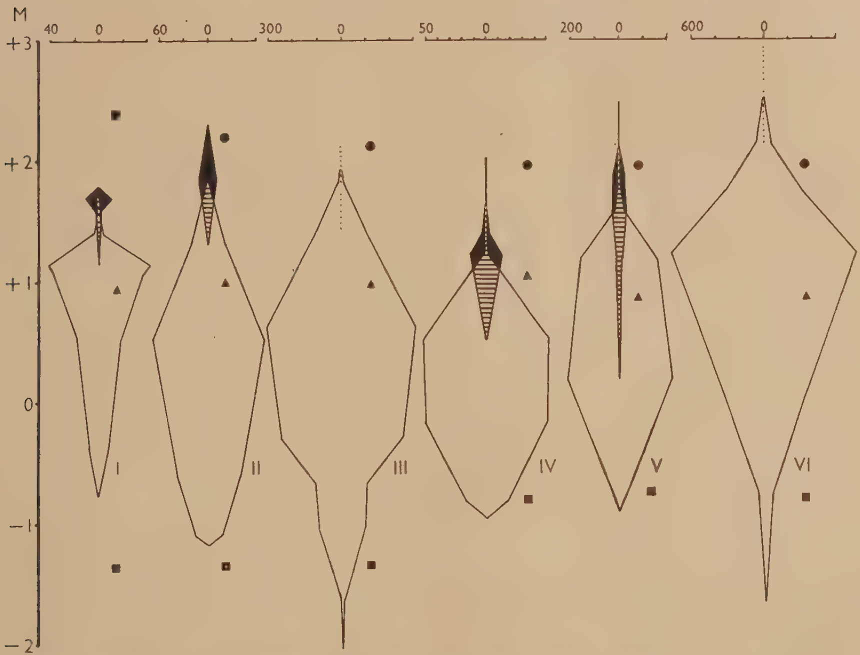


Fig. 1. Interrelation of *Chthamalus stellatus* (black) and *Balanus balanoides* (white) at a series of localities in Scotland. Quantities are measured in grammes (dry weight) of tissue per square metre. Levels (in metres) are referred to local mid-tide level. The approximate heights of other local levels are indicated as follows: mean low-water neap tides ■; mean high-water neap tides ▲; mean high-water spring tides ●. I, Òb Allt an Daraich, Skye; II, Port na Cullaidh, Elgol, Skye; III, Seana Chamas, Ross; IV, Bay of Stoer, Sutherland; V, Geodha Chobhair, Sutherland; VI, Skullomie, Sutherland.

The extent of the competition between *Chthamalus* and *Balanus balanoides*, both for space and for food, remains unknown. The food of each species requires investigation. But in localities where both species flourish there must certainly be competition for space. Denudation of the rock takes place largely during winter as a result of storms, and since *B. balanoides* spat settle in early summer, whereas *Chthamalus* spat do not settle until autumn or winter, the *Balanus* will have time to become well established before the *Chthamalus* appear. In the absence of other disturbing factors this would favour a predominance of *Balanus*, and it probably does actually do so in regions where both species are common, and especially in the lower part of the shore. This effect may quite probably determine the lower limit of *Chthamalus* in these localities.

However, some important factor, other than competition with *Balanus balanoides*, must be operative. This is shown by the fact that in certain localities the lower limit of *Chthamalus* is above the upper limit of *Balanus balanoides*. For instance, as shown in Fig. 1, at Òb Allt an Daraich, in Skye, there was a zone a few centimetres wide of fairly abundant *Chthamalus*, below which there was an almost bare zone several centimetres wide with hardly any barnacles of either species; and below this again *Balanus balanoides* was abundant. Thus the two species intermingled only to a very slight extent. Fischer also (1928) has written (translation) that "at the Point of Granville, at the margin of their geographical distribution, the *Chthamali* are practically restricted to levels which are above the limit of *B. balanoides*...". In these localities it must be presumed that the lower limit of *Chthamalus* is determined by some harmful effect of excessive immersion in sea water (see below, p. 534).

In addition, the lower limit of *Chthamalus* varies with geographical situation. For instance, at the western extremity of the English Channel the vertical distribution embraces the whole littoral region, but as *Chthamalus* approaches the limit of its geographical distribution eastwards in the English Channel, so its lower limit rises (Fischer-Piette, 1936). For geographical reasons it is not possible to demonstrate this effect so clearly up the west coast of Britain as the northern limit of distribution of *Chthamalus* is approached; but the data illustrated in Fig. 1 are sufficient to show that a similar effect exists. In the west of Scotland (e.g. Skye) *Chthamalus* is probably approaching its limit of tolerance of low temperature (see p. 530); whereas in the middle region of the Channel it is near the limit of adequate penetration eastwards of Atlantic water (see p. 528). It is of course possible that either of these factors might exert a stronger influence nearer low water, thereby restricting the *Chthamalus* to the higher levels where such influence was less. This may well be true at the Point of Granville. But at Skye by far the lowest temperature will be experienced during the period when the barnacles are left exposed to the air (in winter), and not when they are covered with water. Therefore at Skye it might be expected that if temperature were the only factor concerned the *Chthamalus* would be restricted to the lower levels, where they would be exposed for the shortest periods to the cold air. It therefore became necessary to postulate that the lower limit of *Chthamalus* is determined by a harmful effect of excessive immersion, and that *Chthamalus* is more sensitive to this influence in localities which are unfavourable in some other respect also. Such modifications of sensitivity will be discussed later (p. 534). It should be realized that it is not possible to distinguish between a harmful effect of immersion and a beneficial effect of emersion. For convenience we have followed the former interpretation. This factor appears to exert a strong influence on *Balanus balanoides* also (Moore, 1935, p. 288).

Upper limit of vertical distribution

The upper limit of *B. balanoides*, when not elevated by splash nor (possibly) depressed by *Chthamalus*, is almost exactly at high water of mean neap tides (Fischer-Piette, 1929; Moore, 1935). That of *Chthamalus* is regularly higher, but information from localities undisturbed by splash is scanty. In Loch Sween the upper limit is near high water of spring tides (Kitching, 1935).

In most of the districts where both barnacles occur their zones overlap, and it is questionable whether or not the upper limit of *Balanus balanoides* may be depressed by the competition of *Chthamalus*. Actually there is no evidence of such an effect. From a comparison of the vertical distribution of the two species in regions where *Chthamalus* is relatively scarce (Fig. 1, p. 525 of this paper) and in regions where it is as abundant as *Balanus* (Moore, 1936, Fig. 4, p. 705), it appears that the effect of the occurrence of *Chthamalus* within the *Balanus* zone is to decrease the abundance of *Balanus*, but not to exclude *Balanus* completely. The nature of the competition between the two species is unknown. If it were merely competition for available space on which to settle, the *Balanus* would be the more likely to preponderate, as already suggested. It might, on the other hand, be a case of competition for the available food. Furthermore, at Plymouth *B. balanoides* is approaching a region which is apparently unfavourable to it. This is indicated by the fact that its progressive decrease in numbers westwards in the English Channel is accompanied, towards the extreme limit of its geographical distribution, by a failure of those individuals which survive to spawn. This has been found elsewhere (Moore, 1935, p. 290) to be an indication of unfavourable conditions. This might be expected to result in a decreased range of tolerance of *B. balanoides* towards certain other environmental factors. On the other hand, *Chthamalus* encounters a progressively more congenial environment westwards down the English Channel (see p. 526), and might therefore show an accompanying extension in range of tolerance for such factors. If then, owing to overcrowding, the two species are in conflict for a limited amount of food, the one with the greater tolerance for adverse conditions may be expected to survive, and to predominate over the less tolerant.

RELATION TO ATLANTIC WATER

It has long been known that certain planktonic animals are characteristic of the enclosed waters of the North Sea, English Channel, and Irish Sea, whereas quite different ones characterize the open waters of the Atlantic and the western coasts of Ireland and Scotland washed by them. Russell (1935, 1936) has shown how some of these, and in particular *Sagitta elegans*, may be used as indicators of the movements of Atlantic water in and out of the mouth of the English Channel. An examination of the geographical distribution of *Chthamalus*, as shown in Fig. 2, makes it apparent that this species also is limited to those shores which are bathed by Atlantic water, being absent from the North Sea, upper Irish Sea, upper Bristol Channel, and eastern half of the English Channel. The only other instance, of which we are aware, of a non-planktonic organism for which a connexion has been suggested between geographical distribution and the presence of Atlantic water is *Echinus esculentus*. The occurrence of this species between tidemarks is, according to Reid (1935), limited to coasts bathed by water of Atlantic characters; although *E. esculentus* is more widely distributed at deeper levels. A comparison of the distributions of *Sagitta elegans*, intertidal *Echinus esculentus*, and *Chthamalus stellatus* reveals the following differences:

(1) In the English Channel *Chthamalus* extends plentifully up to Plymouth, and in small numbers up to Swanage; the eastern limit of *Sagitta elegans* fluctuates from the Scilly Isles eastwards; and intertidal *Echinus* only reach the Scilly Isles and the extreme tip of Cornwall.

(2) In the Irish Sea from its southern entrance *Chthamalus* penetrates farther northwards than does intertidal *Echinus*; *Sagitta elegans* occurs throughout the Irish Sea.

(3) In the Irish Sea from its northern entrance *S. elegans* and intertidal *Echinus* extend southwards to the Isle of Man, whereas *Chthamalus* does not come south of the Mull of Kintyre, as far as we know.

(4) In the North Sea, in its northern entrance, *Sagitta elegans* and intertidal *Echinus* penetrate a considerable distance southwards, whereas *Chthamalus* stops short at Dunnet Head (at the north-east corner of Scotland).

The explanation of these differences probably lies in the fact that the geographical ranges of *Sagitta elegans* and of *Echinus esculentus* extend northwards far beyond the British Isles; whereas *Chthamalus* reaches its northern limit in the north of Scotland, where it is probably limited by temperature. The unfavourable temperature conditions in the northern Irish Sea and in the north of Scotland probably render *Chthamalus* more sensitive to decrease in proportion of Atlantic water than it is in the warmer southern Irish Sea and English Channel; whereas *Sagitta elegans* and *Echinus*, not being on the edge of their geographical range, are not so affected. It must also be realized that *Sagitta elegans*, being planktonic, has a distribution that fluctuates considerably from time to time.

At present there is little or no clue as to what is the character which renders Atlantic water more favourable to *Chthamalus* than the water of an enclosed sea. It cannot be temperature, since this must be considerably higher on the Isle of Man, where *Chthamalus* is not found, than in the north of Scotland, where *Chthamalus* does occur. Similarly it cannot be salinity, since the

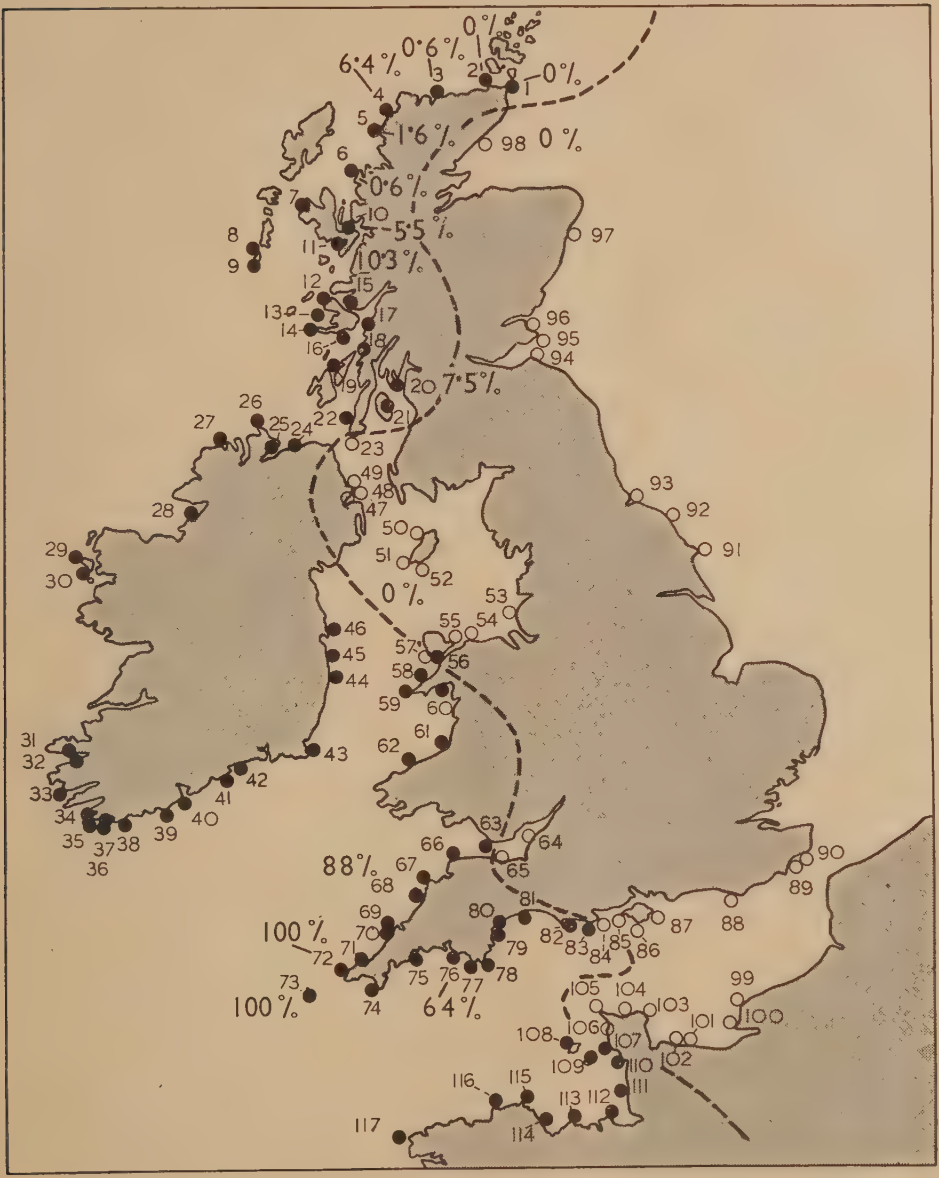

0%
0·6%
6·4%
0%
1·6%
0%
0·6%
5·5%
10·3%
7·5%
0%
88%
100%
100%
64%
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106
107
108
109
110
111
112
113
114
115
116
117

Fig. 2. The geographical distribution of *Chthamalus stellatus*. ○ indicates absent; ● indicates present. Numbers of stations (see Table I) are given in smaller type; the numbers in larger type represent the percentage by weight of *Chthamalus* in the total population of barnacles (*Chthamalus* and *Balanus balanoides*) between tide marks.

difference in salinity between the waters around Plymouth and those near Swanage is quite negligible in comparison with the range of salinity which *Chthamalus* tolerates in the estuary of the river Tamar at Plymouth. Perhaps it is the same unknown factor which Fischer-Piette (1936) has postulated to explain the preference of certain littoral species for regions which jut out into the neighbourhood of deep water, and of others for embayed regions.

EFFECTS OF TEMPERATURE, SALINITY, HYDROGEN ION CONCENTRATION, AND CURRENTS; PENETRATION UP ESTUARIES

Very little is known about the tolerance of *Chthamalus* for temperature. Moore (1935) has recorded a temperature of 36·3° C. within the mantle cavity of one *in situ* on the rocks during a low-tide period, and an even higher temperature could almost certainly be attained on a really hot day. No doubt a time factor would enter into any question as to the highest temperature consistent with survival. As regards the influence of low temperature, *Chthamalus* reaches its northern limit in the north of Scotland, where the February sea-surface temperatures, as given in Deutschen Seewarte Hamburg (1927), are about 6° C., although no doubt considerably lower temperatures occur on the shore itself. *Balanus balanoides*, on the other hand, extends northwards to the region where the shore is frozen in winter, and appears to be limited more by the mechanical action of the ice than by the low temperature.

The figures given for the salinity range tolerated by *Chthamalus* are of doubtful value for two reasons. A barnacle can close its aperture and so protect itself from a temporary lowering of the salinity of the surrounding water. And, in addition, minimal figures for salinity usually refer to the time of low water in the particular part of the estuary in question, whereas *Chthamalus* is usually restricted to a zone near the level of high water, and so is only covered by water of very much higher salinity. No figures are available for the minimal salinity which will allow either survival or feeding.

For the range of hydrogen ion concentration which *Chthamalus* can tolerate there are again no adequate figures. Fischer (1928) has recorded that *Chthamalus* can endure *p*H 9·0.

Wave action is favourable to *Chthamalus*, just as it is to *Balanus balanoides*, but water movement produced by a current can take the place of wave-produced movement. According to Fischer (1928) water movement produced in one way or the other is essential for its survival, and certainly we have found that *Chthamalus* does not survive nearly so well as *Balanus balanoides* in a tank supplied with running water and a tidal rise and fall but without wave action or a strong current. However, in Loch Sween, where conditions are for some unknown reason particularly favourable (Kitching, 1935), *Chthamalus* lives in extremely sheltered places where the current is slight. *Chthamalus* can also survive very muddy water, as for instance in the Tamar estuary.

The strong modifying influence which variation in one factor may have on the degree of tolerance of a given species for another factor is well illustrated by the relative penetration of *Chthamalus* and *Balanus balanoides* into different estuaries. In the lochs on the west coast of Scotland, where *Chthamalus* is near its northern limit, and may therefore be considered as living under generally less favourable conditions than *Balanus balanoides*, the latter penetrates usually to the extreme head of the lochs, if the shores are not too weed-grown, whereas *Chthamalus* usually stops short much nearer to the open sea. It may be either shelter from wave action or low salinity for which the tolerance of *Chthamalus* is here reduced. Farther south, in the Plymouth region, where *Chthamalus* and *Balanus balanoides* occur in more or less equal numbers, both species penetrate the estuaries of the Tamar and Avon to the same extent. Still farther south again in the neighbourhood of Roscoff, *B. balanoides*, which is here at the southern margin of its geographical range, is confined to wave-beaten rocks on the open shore, whereas *Chthamalus*, which is nearer to the centre of its range, extends far up the estuaries into the region occupied by the brackish water alga *Fucus ceranoides*.

Nature of Substratum

The distribution of *Chthamalus* along the coast of the "Isle" of Purbeck (Dorset) was studied in considerable detail, since here *Chthamalus* reaches the eastern limit of its distribution in the English Channel. However, this investigation was complicated by changes in the lithology. The chief rock formations contributing to the shore of the Isle of Purbeck are the Kimmeridge clay, Portland stone, Purbeck stone, Wealden sands, lower greensand, and chalk (Strahan, 1898). Of these only the harder rocks form substrata suitable for barnacles. The Portland stone (a hard limestone), Purbeck stone (also limestone), and chalk reach the shore at various positions along the coast, and *Chthamalus* was found to show a marked preference for Portland stone (Table II). On chalk it was only recorded on the sheltered sides of boulders or on flints. *Balanus balanoides* also was usually absent from chalk, especially when this was covered with green algal slime, but was plentiful on the clean chalk of the Old Harry Rocks. In other localities the abundance (or otherwise) of *B. balanoides* corresponded fairly closely with that of *Chthamalus*. The most likely alternative explanations of the undesirability of chalk are either (more probably) that it affords insecure holding (either for the larvae or for the adults) because of its smooth or even slimy surface, or that being porous it allows the barnacles to be desiccated from below in dry weather.

At two stations on the Purbeck coast both *Chthamalus* and *Balanus balanoides* were present in sufficient numbers for a detailed examination to be made of their vertical distribution. On the eastern promontory of Lulworth Cove the levels of maximal population density of the two species are separated by a vertical distance of about $1\frac{1}{2}$ m., and in the region of overlap of the two zones both species are very sparse. This seemed to indicate that the lower limit of *Chthamalus* was here in no way influenced by the competition of *Balanus balanoides*, but was on the other hand determined by "excessive immersion", just as is already believed to apply in northern Scotland. However, such a conclusion, though possibly correct, does not necessarily follow in this instance. The rock surface at Lulworth is much rougher near the level of high water of spring tides than it is lower down, and *Chthamalus* here shows a marked preference for rough patches of rock. It is therefore possible that towards lower levels sites suitable for *Chthamalus* become progressively fewer.

TABLE II

Locality*	Rock	Nature of surface	*Chthamalus*	*Balanus balanoides*
Swyre Head†	Upper chalk	Smooth, rather slimy chalk	On flints only, sparse	Absent
Durdle Door (west side)	Purbeck stone	Generally smooth	In cracks only	In cracks only
Lulworth Cove (west side)	Portland stone	Variable	Chiefly in crevices	Chiefly in crevices
Lulworth Cove (east side)	Portland stone	Variable	Plentiful in hollows, scarce on open rock	Plentiful
Arish Mell Gap (west side)	Upper chalk	Chalk boulders	Sparse; usually only on landward side of boulders	Sparse; usually only on landward side of boulders
Arish Mell Gap (east side)	Upper chalk	Nearly vertical; smooth, green and slimy	Only one specimen found	Absent
Tilly Whim	Portland stone	Variable, chert bands	Plentiful in hollows and on chert bands	Plentiful
Old Harry Rocks	Upper chalk	Smooth	Absent	Plentiful

* Localities are given in geographical order, from west to east.

† This headland is about three-quarters of a mile west of Durdle Door, and must not be confused with another "Swyre Head" farther east.

The influence of lithology and of texture of rock surface was more strongly marked on the cliffs below the Tilly Whim caves, near Swanage. Here the bedding planes are horizontal and there is therefore a vertical succession of various bands of limestone and chert, each weathered at its surface to a characteristic texture. As will be seen from Fig. 3 and Table III, the vertical distribution of *Chthamalus* does not conform to the usual arrangement of a belt with the maximal population density near the middle, and regions of less density above and below. There are here three levels of high population density, namely, bands A, E, and G, of which E and G are especially thickly populated. E and G are hard cherty bands, with coarse-textured surface weathered in an angular way; and the surface of A is also rather coarse. D, which also has a considerable population of *Chthamalus*, has coarse cherty nodules in it. On the other hand, the bands with relatively smooth surfaces, B, C, and F, have small populations of *Chthamalus*. It is noticeable also that

Chthamalus is specially abundant in certain small upward-facing pockets in the surface of band A, although the reason for this remains doubtful.

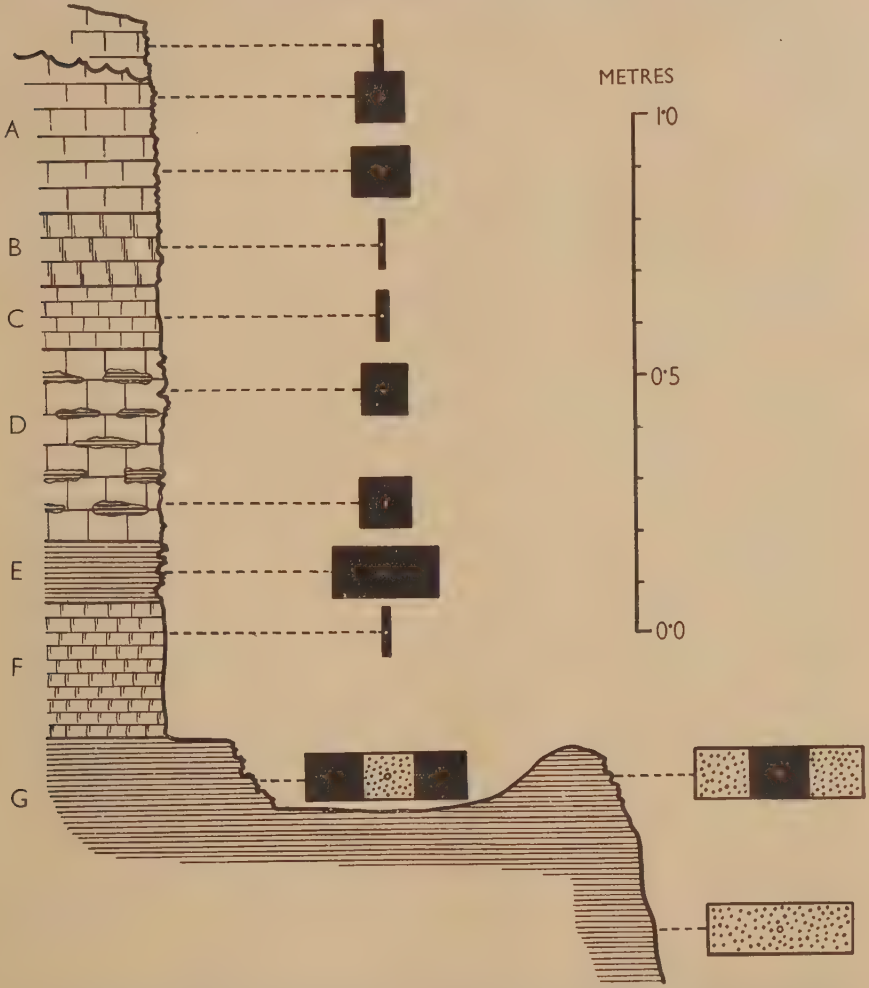


Fig. 3. The vertical distribution of *Chthamalus* (solid black) and *Balanus balanoides* (stippled) in relation to lithology at Tilly Whim, near Swanage, Dorset. For explanation of lettering see Table III. Brick pattern indicates limestone and horizontal shading indicates chert. The texture of the rock surface is indicated diagrammatically.

It appears from these observations that *Chthamalus* prefers a hard rough limestone to a soft smooth one, but it can exist on the latter in positions sheltered from violent wave action. Hatton (1938), in an experiment on

Balanus balanoides, found that the larvae failed to settle on polished marble except in depressions or scratches in the surface. He suggested that they were dragged away by water currents. On the other hand, it has also been shown (Kitching, 1935) that an excessively coriaceous surface is unfavourable to *Chthamalus*. It is also clear that on limestone shores, where the texture of the rock surface is liable to show progressive changes from high water of spring tides downwards, it is necessary to interpret with great caution observations of the vertical distribution of littoral organisms.

TABLE III

			Mean no. of barnacles per m.^{2}	
Band	Nature of rock	Nature of surface	*Chthamalus*	*Balanus balanoides*
A (top)	Limestone	Coriaceous	125	0
A (upper half)	Limestone	Coriaceous	620	0
A (lower half)	Limestone	Coriaceous	750	0
B	Limestone	Less coriaceous	80	0
C	Limestone	Smooth, greenish	180	0
D (upper part)	Limestone and chert	Uneven	600	0
D (lower part)	Limestone and chert	Uneven	670	0
E	Chert	Angular and creviced	1370	0
F	Limestone	Rather smooth, greenish	110	0
G	Chert	Hard, angular	2075	650
G (same level at outer edge of shelf)	Chert	Hard, smoother	730	2170
G (lower down, on outer side of shelf)	Chert	Hard, smoother	0	1875

N.B. The above figures can only be regarded as very rough. Each mean has been compiled from between three and ten counts. Each count was made on a separate 10 × 10 cm. square of rock surface, selected as typical of the band in question.

MODIFICATIONS OF THE RANGE OF TOLERANCE TOWARDS ENVIRONMENTAL FACTORS

In a number of instances, in attempting to explain the distribution of *Chthamalus*, we have suggested that its ability to endure conditions which are unfavourable in respect of one environmental factor may be modified by the action of another factor. For instance, its resistance to excessive immersion is thought to be reduced by deficiency of Atlantic water in the English Channel and probably by low temperature in the north and west of Scotland (p. 526). In addition, its tolerance of sheltered water and its power of penetration up estuaries are similarly reduced in both these regions. On the other hand, in the northern part of the Sound of Jura (west coast of Scotland), and in the lochs opening into it, *Chthamalus* is markedly more tolerant of environmental factors than it is on the neighbouring parts of the coast. In this quite restricted favourable area *Chthamalus* penetrates far into extremely sheltered arms of the sea lochs, and is very much more abundant than in wave-exposed, and therefore presumably favourable, situations on the western (Atlantic) coast of Jura. This curiously local vigour of *Chthamalus* is difficult to explain, but is possibly connected with the abnormal tidal conditions in this area, which are such that the *Chthamalus* zone remains uncovered but subject to splashing for prolonged periods. Whatever may be the explanation, *Chthamalus* appears in this area to be unusually tolerant of various environmental factors. Some beneficial influence appears to ameliorate locally an environment which in some other respect (probably temperature) is none too satisfactory.

It might in certain cases be argued that there is no proof that one factor may modify the tolerance of *Chthamalus* towards another factor. For instance, as already suggested, unsuitable water might prove especially adverse in the lower part of the shore, and so raise the lower limit of *Chthamalus*. It is, however, difficult to frame plausibly any comprehensive explanation of the distribution of *Chthamalus* in terms of the direct action of environmental factors upon an organism with unvarying limits of tolerance. Why, for instance, should *Chthamalus* be able to withstand in Loch Sween or in the Tamar conditions towards which, on the north-west coast of Scotland or in the English Channel, it cannot make any approach?

Although the idea of modified tolerance seems obvious enough, we have not been able to find many comparable examples. The tolerance of *Procerodes* (= *Gunda*) *ulvae* for low salinity is dependent on the presence of sufficient calcium in the external medium (Pantin, 1931), but this is probably a direct effect of the calcium ion on the permeability of cell membranes. Although it is not possible to decide definitely until the interplay of all the various factors involved has been analysed, it seems that in *Chthamalus* the modification of tolerance takes effect by a change in the general vigour of the organism, rather than by the direct action of one factor on some particular part of the organism which is especially susceptible to the influence of another factor.

Perhaps a more satisfactory parallel example is provided by the effect of competition with one another on the temperature range of fresh-water planarians. Beauchamp & Ullyott (1932), working in parts of eastern and southern Europe, investigated the distribution of *Planaria montenegrina* and *P. gonocephala* in swiftly flowing streams in which the temperature of the water increased progressively from the source downwards. In streams in which both species occurred, *P. montenegrina* occupied an upper section extending from the source down to where the temperature reached 13–14° C., and *P. gonocephala* ranged from this latter level downwards. There was scarcely any overlapping of the two species. But in certain streams, from which *P. montenegrina* was absent, *P. gonocephala* extended up to sources as cold as those normally occupied exclusively by *P. montenegrina* (e.g. 8·5° C.).

And in certain streams, from which *P. gonocephala* was absent, *P. montenegrina* extended down to parts of the stream which would, in the presence of the other species, have been too hot (16–17° C.). Thus competition seems to influence the range of temperature tolerated by these planarians.

In addition, Broekhuysen (1936) has recorded a decrease in tolerance of low salinity in *Carcinus maenas* (the shore crab) in winter, as compared with summer when the temperature is higher.

In general, therefore, it seems permissible to postulate that departure from the optimal condition for one environmental factor may reduce the tolerance range of a species for a second factor. It seems possible that this effect will be found to play an important part in the distribution of organisms in an environment such as the shore, where conditions are so exceptionally varied.

GROWTH RATE

Hatton (1938), in a supplement to previous work of Hatton & Fischer-Piette (1932), has given figures relating to the growth of newly settled *Chthamalus* at different levels, during a period of 18 months. In a wave-exposed locality the lengths (mm.) attained were:

	1930–1 spat		1931–2 spat	
	After 9 months	After 18 months	After 9 months	After 18 months
Slightly above high water of neap tides	2·6	5	2	4·1
Slightly below high water of neap tides	3·6	4·1	2·5	3·6
Mid-tide level	4·1	4·2	2·7	3·4

Thus in the first year growth was greatest at the lowest level, but in the second year at the highest. However, in a more sheltered locality growth was greatest at the highest level in both years. Seasonal variation in growth rate was slight.

An attempt was made to estimate the growth rate of *Chthamalus* at Drake's Island, Plymouth, by means of periodic measurements of a number of barnacles belonging to several year groups at three different levels on the rocks, the individual barnacles being recognized from a photograph. Unfortunately, the extreme irregularity of their outline, and the smallness of the growth observed, introduced too great an error to permit any deductions on seasonal variation in growth rate to be made, so that only the total growth for the period is used here. Hatton (1938), however, found little variation in growth rate throughout the year. The three levels selected represent the upper, middle and lower regions occupied at Plymouth by *Chthamalus*, and it is unfortunate that there is so little difference in level between them. It would be better if the experiment could be repeated somewhere where *Chthamalus* occupies a wider zone on the shore. The results obtained during 10 months' growth are shown in Fig. 4. All sizes of barnacle show definitely greater growth rates at lower levels. The newly settled 1936 spat, when measured in December 1936, averaged $\left(\frac{\text{length}+\text{breadth}}{2}\right)$ 1·61, 2·22 and

2·19 mm. respectively at the upper, middle and lower station, and in October 1937 these spat had grown to 3·07, 3·99 and 4·18 mm. respectively. On the same date the 1937 spat averaged 0·65, 0·79 and 1·15 mm. From the measurements made on Drake's Island the following averages were derived for the size $\left(\frac{\text{length}+\text{breadth}}{2}\right)$ of *Chthamalus* of various ages at the three levels in question, but it must be emphasized that these values are no more than very rough approximations:

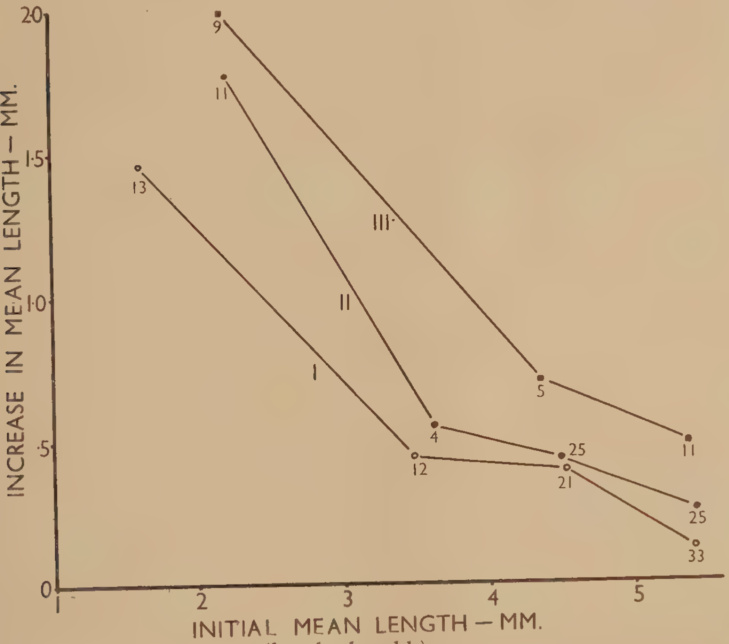


Fig. 4. Increase in mean length $\left(\frac{\text{length}+\text{breadth}}{2}\right)$ of *Chthamalus stellatus* at three levels at Drake's Island, Plymouth, between December 11, 1936 and October 20, 1937. The figures alongside the curve indicate numbers of specimens. Levels: I, +1·36 m. (O.D.); II, +0·81 m. (O.D.); III, +0·41 m. (O.D.).

	Number of months since settlement of spat			
Level*	12	24	36	48
+1·36 m.	2·0	3·7	4·2	4·6
+0·81 m.	3·8	4·5	5·0	5·4
+0·41 m.	3·9	5·0	5·6	6·0

* Levels above ordnance datum.

Whereas at Plymouth the rate of growth remained greatest at the lowest level, at St Malo there appears to have been some unfavourable influence at the lower levels which operated progressively more severely as the *Chthamalus* grew older, and which was also rendered more effective by lack of wave action. Further observations are desirable from localities near the centre and at the edge of the geographical range of *Chthamalus*.

MORTALITY RATE

Figures for the mortality rate of barnacles are somewhat scarce. In the sublittoral region, although in some places the barnacles may persist for long periods, in general it is probable that they appear as early colonists of areas denuded by winter storms and other means, but that they are soon smothered by later arrivals such as ascidians, sponges, and algae (Kitching, 1937). The mortality rate of *Balanus balanoides* found by Moore (1934) for a small number of individuals of over 4 months old was 35% per annum in the lowest levels and 3% in the uppermost. Hatton (1938) has also found a higher mortality rate for *B. balanoides* at the lower levels. The figures for *Chthamalus* on Drake's Island were as follows:

Level	No. of individuals	Mortality rate % per annum
+1·36 m. O.D.	71	3·3
+0·81 m.	70	16·6
+0·41 m.	30	46·5

Hatton (1938) found a mortality rate near St Malo of 24–25% per 20 months around the level of high water of neap tides, and of 96% at about mid-tide level, in a wave-beaten situation. In a sheltered situation the rate was higher.

It is noteworthy that most of the deaths at Plymouth occurred during a period of severe winter gales when the shore showed signs of considerable disturbance, and numbers of *Patella* were found with their shells fractured, apparently by blows from boulders. Probably therefore most of the *Chthamalus* were killed by stones pounded against the rocks by waves.

ENEMIES

The enemies of *Chthamalus* are much the same as those of *Balanus balanoides*, with the difference that where *Chthamalus* occupies a higher zone on the shore it is less liable to be attacked by *Purpura lapillus*. *Purpura* is undoubtedly their chief enemy. In addition no doubt many are killed or fractured by wave-borne stones and then eaten by small carnivores such as crabs and certain amphipods. Some are displaced by *Patella* in its wanderings (Hatton, 1938), and at the lower levels some are smothered by the overgrowth of algae and *Mytilus*. A certain number are probably killed and eaten by crabs and by shore fish such as wrasse. Herring gulls have been found to eat barnacles on occasions, but not in large quantities. Finally, an enemy which may play at the lower levels almost as serious a part as does *Purpura* is the polychaete, *Eulalia viridis*. As we are not aware of any previous record of the attacks made by *Eulalia* on barnacles, a note is given below of observations made by one of us (H. B. M.) at Drake's Island.

On a number of occasions when the shore was visited as the tide was receding, *E. viridis* was observed feeding in considerable numbers on barnacles on those rocks which were still wet, and on which the sun was not shining. After from half an hour to an hour of emersion the *Eulalia* had usually all disappeared. In June 1937, in an area of about 6 sq. m., about twenty *Eulalia* and a single specimen of a species of nemertine were seen feeding on *Balanus balanoides*. The movements of one *Eulalia* were watched in detail. First it moved for some distance across the barnacles. Then it stopped and explored the orifice of one barnacle for a period of a minute or more, during which it several times moved its head away a centimetre or so from the barnacle. It next applied its mouth to the opercular plates of the barnacle, the proboscis not being everted, and after a few seconds one of the plates burst outwards with an audible click. The *Eulalia* then arched its front end off the ground and everted its proboscis downwards into the aperture of the barnacle. For about 5 min. peristaltic movements were visible in the proboscis, and once or twice this was withdrawn for an instant from the barnacle. At the end of this time the worm left the barnacle, and moved off in search of another; and on examination the shell of the barnacle was found to have been completely emptied.

ACKNOWLEDGEMENTS

We gratefully acknowledge the assistance of all those who helped in making the observations recorded in this paper and in obtaining material from the various localities recorded in Table I. We wish to thank in particular the staff of the Plymouth laboratory and the crew of the M.B. *Gammarus*. We are indebted to Professor C. M. Yonge for his criticism of the manuscript.

SUMMARY

Chthamalus stellatus is a littoral barnacle very similar in habitat and general ecological relations to another littoral barnacle, *Balanus balanoides*. In those localities where both species flourish they compete considerably for space, and also possibly for food. The fact that *B. balanoides* settles sooner after the winter storms than does *Chthamalus* probably favours the former.

Chthamalus is characteristically a southern species and *Balanus balanoides* a northern one, but the north and south ranges of the two species overlap in the British Isles and in France. The determining factor is presumably temperature.

Chthamalus is an Atlantic species, and *Balanus balanoides* is more characteristically a North Sea species. The essential factor in Atlantic water remains unknown, although in respect of a need for Atlantic water *Chthamalus* resembles *Sagitta elegans* and intertidal *Echinus esculentus*.

Except in especially favourable districts (see below), *Chthamalus* is usually

restricted to a zone in the upper part of the shore, whereas *Balanus balanoides* occupies a zone mainly below the *Chthamalus* zone. In certain places where the two zones do not overlap it is clear that the lower limit of *Chthamalus* is determined, not by the competition of *Balanus balanoides*, but by some adverse effect of excessive immersion.

Towards its northern limit of geographical distribution and towards regions where Atlantic water is deficient, *Chthamalus* extends less far down on the shore and less far into sheltered waters and estuaries. It seems that its tolerance of excessive immersion and of certain conditions characteristic of bays and estuaries becomes reduced in an environment unfavourable in respect of Atlantic water or temperature.

On Drake's Island, Plymouth, the growth rate and rate of mortality of *Chthamalus* were found to be greater at the lower levels.

The chief enemy of *Chthamalus*, as of *Balanus balanoides*, is *Purpura* (=*Nucella*) *lapillus*. The polychaete *Eulalia viridis* was observed feeding on *Balanus balanoides*. Many barnacles are probably killed by stones pounded against them by the waves.

REFERENCES

BASSINDALE, R., 1936. The developmental stages of three English barnacles, *Balanus balanoides* (Linn.), *Chthamalus stellatus* (Poli), and *Verruca stroemia* (O. F. Müller). *Proc. Zool. Soc. London*, 1936, pp. 57–74.

BEAUCHAMP, R. S. A. & ULYOTT, P., 1932. Competitive relationships between certain species of fresh-water triclads. *Journ. Ecol.*, Vol. XX, pp. 200–8.

BROEKHUYSEN, G. J., 1936. On the development, growth, and distribution of *Carcinides maenas* (L.). *Arch. Néerland. Zool.*, Vol. II, p. 257–399.

DEUTSCHEN SEEWARTE HAMBURG, 1927. *Atlas für Temperatur, Saltzegehalte und Dichte der Nordsee und Ostsee.* Hamburg.

FISCHER, E., 1928. Sur la distribution géographique de quelques organismes de rocher le long des côtes de la Manche. *Trav. Lab. marit. Saint-Servan*, Fasc. II, 16 pp.

—— 1929. Recherches de bionomie et d'océanographie littorales sur la Rance et le littoral de la Manche. *Ann. Instit. Océanogr.*, N.S., Vol. V, pp. 202–429.

FISCHER-PIETTE, E., 1932. Répartition des principales espèces fixées sur les rochers battus des côtes de la Manche, de Lamnion à Fécamp. *Ann. Instit. Océanogr.*, N.S., Vol. XII, pp. 107–213.

—— 1936. Études sur la biogéographie intercotidale des deux rives de la Manche. *Journ. Linn. Soc.*, Vol. XL, pp. 181–272.

HATTON, H., 1938. Essais de bionomie explicative sur quelques espèces intercotidales d'algues et d'animaux. *Ann. Instit. Océanogr.*, N.S., Vol. XVII, pp. 241–348.

HATTON, H. & FISCHER-PIETTE, E., 1932. Observations et expériences sur le peuplement des côtes rocheuses par les cirripèdes. *Bull. Instit. Océanogr. Monaco*, No. 592, pp. 1–15.

KIDD, F. L., PYEFINCH, K. A. & BUTLER, P. M., 1935. The ecology of Bardsey Island: topography and types of environment. *Journ. Animal Ecol.*, Vol. IV, pp. 231–43.

KITCHING, J. A., 1935. An introduction to the ecology of intertidal rock surfaces on the coast of Argyll. *Trans. Roy. Soc. Edinb.*, Vol. LVIII, pp. 351–74.

—— 1937. Studies in sublittoral ecology. II. Recolonization at the upper margin of the sublittoral region; with a note on the denudation of *Laminaria* forest by storms. *Journ. Ecol.*, Vol. XXV, pp. 482–91.

MARRAT, F. P., 1886. Notes of the Cirripedia of the L.M.B.C. district. *Fauna of Liverpool Bay*, Rep. I, p. 209. London.

MOORE, H. B., 1934. The biology of *Balanus balanoides*. I. Growth rate and its relation to size, season, and tidal level. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 851–68.

—— 1935. The biology of *Balanus balanoides*. III. The soft parts. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 263–77.

—— 1936. The biology of *Balanus balanoides*. V. Distribution in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 701–16.

PANTIN, C. F. A., 1931. The adaption of *Gunda ulvae* to salinity. *Journ. Exp. Biol.*, Vol. VIII, pp. 63–94.

PRENANT, M. & TEISSIER, G., 1924. Notes éthologiques sur la faune marine sessile des environs de Roscoff. Cirripèdes, Bryozoaires, Hydraires. *Trav. Stat. Biol. Roscoff*, Vol. II, pp. 1–49.

REID, D. M., 1935. The range of the sea urchin *Echinus esculentus*. *Journ. Animal Ecol.*, Vol. IV, pp. 7–16.

RUSSELL, F. S., 1935. On the value of certain plankton animals as indicators of water movements in the English Channel and North Sea. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 309–32.

—— 1936. Observations on the distribution of plankton animal indicators made on Col. E. T. Peel's Yacht "St George" in the mouth of the English Channel, July 1935. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 507–22.

STRAHAN, A., 1898. The geology of the Isle of Purbeck and Weymouth. 278 pp. *Memoirs of the Geological Survey*. London.

WALTON, C. L., 1915. The shore fauna of Cardigan Bay. *Journ. Mar. Biol. Assoc.*, Vol. X, pp. 102–13.

ON A NEW SPECIES OF *GAMMARUS* (*G. TIGRINUS*) FROM DROITWICH DISTRICT

By E. W. Sexton, F.L.S.

With an Appendix by L. H. N. Cooper, D.Sc., F.I.C.

From the Plymouth Laboratory

(Plates IV–VI)

The new species of *Gammarus* here described was first noted in 1931 by Prof. H. Munro Fox, to whom I am indebted for the opportunity of examining it. He found it in abundance in the Droitwich district, living in the brackish waters of the River Salwarpe near the town, in the Canal, and in Wyken Slough near Coventry.

Droitwich is an inland town in Worcestershire, situated on the Salwarpe, a tributary of the River Severn. It is famous for its natural alkaline brine springs, and it is these which make the waters of the district saline.

In August 1938 a quantity of fresh material was collected by Mr G. M. Spooner and Miss M. Mare, who visited several localities in Worcestershire, Warwickshire, and north Gloucestershire. The species was found in numbers at Wyken Slough and at Droitwich (River Salwarpe), and in small numbers in the River Avon at Tewkesbury. The two former localities were already known to Prof. Munro Fox as haunts of *Gammarus tigrinus*. Tewkesbury was visited because of the occurrence of some unknown amphipods in a collection made by Mr G. I. Crawford in 1935. In the light of the fresh material obtained, these specimens are now recognized as the young of *G. tigrinus*. No new localities were discovered. Those visited are listed in the following table, which also gives the occurrence of the only other species of *Gammarus* collected, namely, *G. pulex*.

Locality	*G. tigrinus*	*G. pulex*
River Chelt, Gloucester-Tewkesbury road	o	Abundant
River Avon, Tewkesbury	Sparingly	Scarce
River Arrow, Alcester	o	Scarce
Stratford Canal, north-west of Stratford-on-Avon	o	o
Wyken Slough, north-east of Coventry	Abundant in the lake and connecting streams	o
Oxford Canal, near the above	o	Scarce
River Blythe, Patrick Br.	o	o
Earlswood Reservoir, Canal on north-east side	o	o
Earlswood Reservoir, outflowing stream	o	Numerous
Droitwich, River Salwarpe at exit from town	Abundant	o

(o = species looked for and not found.)

Samples of the water at Wyken Slough, at Droitwich, and at Tewkesbury were taken, and analyses made by Dr L. H. N. Cooper (see Appendix, p. 549). The two former have a high mineral content of peculiar composition, and the latter was found to contain a higher quantity of dissolved matter than is usual in rivers of comparable size.

Mr Spooner supplies the following data on the habitats in which he collected *G. tigrinus*. At Tewkesbury the species was found patchily, at the edge of the river among leaves, roots, and debris around the base of *Glycera aquatica** plants. Here corixids were abundant and *Asellus* common. The few specimens of *Gammarus pulex* obtained were apart from the patches of *G. tigrinus*. Wyken Slough is a shallow lake of about 5 acres extent lying in a hollow on the course of an upper branch of the River Sowe, a tributary of the Avon. It marks a point where Carboniferous, Permian, and Upper Trias strata abut. The bottom consists of black mud, but there is no lack of vegetation round the edges, and the fauna is rich. *G. tigrinus*, *Potamopyrgus jenkinsi*, and a corixid were among the dominant species. The former was sieved in quantity from growths of *Myriophyllum spicatum** and roots of *Oenanthe*: it occurred all round the lake and in both the inflowing and outflowing streams. The River Salwarpe, at the point where the collection was made (on the west side of Droitwich), is a shallow and fairly fast-flowing stream, with a stony bottom deficient in vegetation. The *Gammarus* were collected in numbers from the undersides of stones and bricks lying in the stream. *Potamopyrgus jenkinsi* was present in great abundance—in one place accumulated in such numbers as to form a bottom deposit, in which many *Gammarus tigrinus* were sheltering.

The *Gammarus* collected in the above localities in August were brought back to Plymouth alive and kept under observation in the laboratory. Further consignments of living material were sent by Prof. Munro Fox in November and December 1938.

All the *Gammarus* species which have been studied so far at Plymouth show great adaptability to changes of salinity, provided only that the changes are made very gradually and extended over a considerable period of time. A sudden transference from one medium to the other causes instant death. By working in this way, and with the young rather than with the adult, I have been able to bring, amongst others, the fully marine *G. locusta* to live and breed in fresh water, and, in the reverse direction, *G. pulex* from fresh water to sea water, with no ill effects either during the transition period or afterwards.

The new species has shown an even greater adaptability than the others. Owing to a shortage of the Droitwich water many different mixtures were tried to find the salinity best suited to the animals' needs. This was found to be the "standardized" water used in the *G. chevreuxi* work, namely, one part sea water to four of fresh water from the Plymouth supply, which gives a mixture of about 7‰ salinity. The adults, it is true, died off rather quickly in it, but the young from their matings survived and are still alive and healthy, some in pure Droitwich river water, some in pure standardized, and others in a mixture of half and half. They are not yet mature (February), but that no doubt is due to winter conditions retarding development.

---

* Miss M. Mare det.

Gammarus tigrinus n.sp.

Unless otherwise stated, the following description refers to the fully adult male, and the sizes and proportions given apply only to specimens which have attained the maximum growth.

Colour. The specific name, *tigrinus*, refers to the remarkable colour pattern in the living animal, stripes and bars of dark pigment on a light background.

The body colour is a delicate pale green, yellowish green in the male, bluer in the female. The stripes, of deep indigo blue, run transversely across each segment, and extend to halfway down the sides. In addition to the dark stripe or stripes, each segment is banded posteriorly with a clear yellow, so that the effect, seen dorsally, is of alternating bars of pale green, deep blue almost black, and bright gold. From the lateral view the effect is even more striking. Just below where the stripes end, halfway down the sides, two longitudinal bands of colour run along the whole length of the body. The lower one is darkly pigmented and follows the line of the intestine; the upper one is brilliant red. A colour pattern of this type has not been noted, as far as is known, in any other species of *Gammarus*, and would appear to be peculiar to *G. tigrinus*. In some specimens the red shades off on either side, through orange to pale pink, in others it remains as a sharply defined red band. The usual clusters of "oil globules" in the first three pleon segments are also bright red.

The figure of the whole animal (Pl. IV) was taken from a freshly captured specimen, while the colouring was still vivid. In captivity, a steady loss of colour takes place, particularly in the red; after death, and in preservatives, all traces of it vanish.

Size. Compared with others of the genus, *G. tigrinus* is a fairly large species, the males looking larger than they actually are, by reason of the masses of fine hairs on the appendages. The full-grown male averages from 10·5 to 12·5 mm., the female from 8·5 to 10 mm. These measurements are taken, not, as is frequently done, along the dorsal curve, but with the animal straightened out on a micrometer scale, from the tip of the rostrum to the insertion of the telson.

Sex. The difference between the sexes is much more noticeable than is usual in the genus. All the appendages of the male are larger in proportion, the gnathopod hands, for example, being twice the length of those of the female. The male carries masses of the long fine curved sensory hairs peculiar to this species on its second antenna, first, second, fourth and fifth peraeopods, while the female has none of these, and fewer spines and setae than the male. Breeding appears to continue throughout the year.

The gonads and eggs of the female are dark green in colour. The eggs are comparatively large and numerous; the highest number of young, so far, hatched in one brood in laboratory conditions was 50. There are four pairs of incubatory lamellae, or brood-plates, attached to peraeon segments 2–5, of very unusual proportions, two large and two small. The first is the largest and carries the greatest number of fringing hairs, forty-nine in the specimen figured (Pl. V, fig. 11). The second is almost the same size and shape, with 35 hairs; the third is suddenly very small, narrow, strap shaped, with 22 hairs; whilst the fourth, with 14 hairs, is even smaller and narrower. In another younger female examined, the hairs numbered respectively, 31, 26, 13 and 10.

Owing to its curious conformation the pouch looks only about half the ordinary size of the *Gammarus* pouch, and the eggs when deposited appear to lie farther forward under the peraeon than is usual.

The *body* is slender, with the back evenly rounded. The *cuticle* is microscopically spinulose all over (Pl. VI, fig. 27). The spinules are small and not so produced on the anterior part of the body, giving it a surface like a rough file or rasp, but on the pleon, particularly on the dorsal region, they are much longer, very dense and sharp, and look, under a high power, like a thick prickly fur. Scattered over the body and appendages, and inset either singly or in groups, are numerous sensory processes, in little smooth indentations (see figure).

The *gills* are large, oval in shape, and are carried on peraeon segments 2–7. Two are figured (Pl. V, figs. 7, 12).

Side-plates 1–4 are deeper than the corresponding segments, all with an unusually large number of setae inset on the margins, and fine delicate semi-transparent setae on the under surfaces. The fourth side-plate (which is used as a distinguishing specific character) is longer than it is broad, with the posterior expanded portion rounding off into the inferior margin, and inset with five long setae (Pl. V, fig. 13). The sixth and seventh side-plates are both furnished with fine long setae anteriorly, the seventh being noticeable for the number of serrations and setae behind (see Pl. VI, fig. 17).

Pleon segment 1 (Pl. VI, fig. 18) with 12–14 long delicate setae inset in a row around the anterior angle of the epimeron, is deeply notched behind for the insertion of a seta. In pleon segments 2 and 3 (Pl. VI, figs. 19, 22) the epimeral plates are produced acutely backwards, the second with a number of stout spines and setae on the anterior half, and the third with a row of spines and setae on the inferior margin. The *pleopods* (Pl. VI, fig. 18) are long and slender; the rami are subequal and about twice the length of the peduncle, each with a large basal joint, and about 20 small joints furnished with two long plumose setae apiece. The peduncle of pleopod 3 has a large radiating fan of hairs at the anterior distal angle. One of the cleft spines of the basal joint, inner ramus, is figured (Pl. VI, fig. 20). Pl. VI, fig. 21 shows the unusually elaborate form of the coupling spines in this species.

The *head* is about half as long again as peraeon segment 1, measured along the dorsal line. The rostrum is not produced; the lateral lobes are vertically truncate, the upper and lower angles rounded: there is a rather deep sinus below.

The *eyes* are large and reniform; the ommatidia were about 90–100 in number in the specimen examined; the retinal pigment is black, with the "accessory pigment" forming a white reticulation.

Antenna 1 (Pl. V, fig. 1) is much shorter than antenna 2, being only about three-quarters its length. The first joint of the peduncle is large and broad, and almost as long as the second and third taken together. It carries on its upper surface the "sensory groove" (first noted in *Gammarus chevreuxi*, *Journ. Mar. Biol. Assoc.*, vol. XIII, 1924, p. 386), containing, in the full-grown animal, seven very finely plumose sensory hairs, graduated in size, the longest at the distal end of the groove, each mobile in a little socket. The *primary flagellum* appears to be very fragile; in many specimens it was found broken or regenerating, rarely complete. The longest counted, for the male, consisted of 26–27 joints, with an *accessory flagellum* of 6 joints, the terminal joints in both, minute; for a female of 10 mm. length, the primary numbered 26, and the accessory 6, younger females had 16–23 joints in the one, 4–5 in the other. The *flagellum* is almost glabrous, the setae few and short. Each joint, except the formative proximal and the terminal, carries a small stalked calceolus inset on the inner surface (Pl. V, fig. 2).

Antenna 2 of the male (Pl. V, fig. 3), is noteworthy for the length of the fourth and fifth peduncle joints, the latter being the longer. The fourth carries on either side about 9, the fifth about 11 groups of long flexible setae set fanwise on the outer surface; in addition the fourth joint is furnished with several stout spines on its upper surface, 3 on the outside, in the specimen figured, and 1 on the inner side. The *flagellum* has about 14 joints, each with a group of the long setae on the upper and lower margins. The inner surface of the fourth and fifth joints of the peduncle, and 9—10 joints of the flagellum is clothed with masses of the delicate lightly curled hairs peculiar to this species, set in clusters.

In the female (Pl. V, fig. 4) these hairs are entirely lacking. The flagellum in the 10 mm. specimen referred to above numbered 14 joints.

The *gnathopods* show a great disparity in size and armature between the sexes.

Gnathopod 1: in the male (Pl. V, fig. 5) the hand is oblong oval and the palm crenulate, oblique, with a large truncated median spine. At the palmar angle, the long claw shuts down between the "angle-groups" (Pl. V, fig. 6), with one stout and one short curved spine inset together above the tip on each side, and one short curved spine on the upper surface at the tip, with two underneath.

Gnathopod 2: in the male (Pl. V, fig. 7). The hand is broader in proportion to its length than in gnathopod 1; and the palm is sinuous and crenulate, more nearly transverse. It has the truncated median spine on the margin, and, at the palmar angle, a graduated row of three stout spines on the outer side, and two groups of short curved ones underneath (Pl. V, fig. 8).

None of the characteristic sensory curled hairs are developed on the gnathopods.

In the female there is very little difference in the two gnathopod hands (Pl. V, figs. 9, 10). The palm is more oblique in gnathopod 1. They are only half the length of the hands of the male. Gnathopod 2 carries the first and largest of the brood-plates (Pl. V, fig. 11).

The peraeopods. The most noticeable point about the peraeopods, and one which distinguishes this species from the others of the genus, is the sensory armature. Generally speaking, the sensory hairs peculiar to a species which develop in the male at sexual maturity occur only on the first pair of the peraeopods. In *G. tigrinus* the second, fourth, and fifth as well as the first are all furnished with masses of the curled hairs on the under-surface of joints 4–6. The peraeopods carry also dense clusters of strong flexible setae set fanwise on the margins, and groups of various sized sensory spines, including the slender setiform kind developed on these appendages in *Gammarus*. In addition, a new and hitherto undescribed type of spine, is found on the anterior margins of a few of the joints. This is the "stiletto spine" (Pl. VI, fig. 15) shaped like a stiletto, with a strong flat shaft, broad at the base and tapering off to a pointed end.

The fourth is the longest of the peraeopods. The anterior margins of the basal joints of the three hinder peraeopods (Pl. VI, figs. 14, 16, 17) are inset with stout spines; the margin of the posterior expansion in each has a row of setae of varying lengths; the under surfaces in all three carry numbers of the delicate hyaline setae.

In peraeopod 3, the hind-lobe is free; in 4 and 5 the expansion narrows gradually to end in a group of spines and setae at the distal angle.

The peraeopods of the female resemble those of the male, though smaller in all their parts. They have the same groups of long setae and sensory spines, fewer in number, but none of the curled hairs. The stiletto spines are also present, very poorly developed as compared with the male.

The *uropods.* Uropod 1 (Pl. VI, fig. 23) is the longest of the three, a third as long again as the second (Pl. VI, fig. 24). In the third, outer ramus 2-jointed; inner ramus about two-thirds the length of the outer. Both carry spines, clusters of setae, and long plumose setae of two kinds, those bordering the margins being straight with firm shafts. The second kind are few in number, very fine and flexible, curving over at the tips.

The *telson* (Pl. VI, fig. 26) is cleft to the base. There is a lateral group of one spine and setae on each side, and a group of two spines and setae on the apices.

To summarize briefly, the principal distinguishing characters of the new species, *Gammarus tigrinus*, are to be found:

1. *In the antennae*: antenna 1 shorter than antenna 2; accessory flagellum 5–6 jointed; fourth and fifth joints of peduncle of antenna 2 in the male exceptionally

long, the fifth the longer, flagellum about equal in length to these 2 joints together.

2. *In the gnathopods:* the difference in size of the hands between the adult male and female.
3. *In the peraeopods:* the shape of the fourth side-plate (Pl. V, fig. 13).
4. *In the uropods:* the proportions of the rami in the third, the inner ramus two-thirds the length of the outer.
5. *In epidermal structures:* in particular, in the long curled sensory hairs peculiar to the male of this species, and the positions in which they occur.

APPENDIX

By L. H. N. Cooper

Qualitative examination of waters from the Midlands of England, in which Prof. Munro Fox had found the new species, *Gammarus tigrinus*, described above by Mrs Sexton, showed them to be of unusual composition suggesting the need for a quantitative analysis.

METHODS OF ANALYSIS

Standard methods of analysis were used. Sodium was not determined directly but was calculated as the equivalent of alkali required to satisfy the acid radicals not already taken up by calcium and magnesium. Potassium was not present in considerable amount.

The salts composing "total solids" dried at 180° C. should be anhydrous except for magnesium sulphate which is likely to contain one molecule of water of crystallization. This has been computed for Table I. At 180° C. also, bicarbonate must have been converted to carbonate and allowance has been made for this in calculating the composition of total solids.

The positions of the waters sampled in August 1938 have been described by Mrs Sexton. Those from the Droitwich river (River Salwarpe) and from Wyken Slough, which resemble neither diluted sea water nor the hard waters found in limestone districts, must have their origin in the salt springs of the district. The chloride, although not proportionately as high as in sea water, is yet remarkable for an inland stream. Calcium and magnesium are not very much greater than they would be in diluted sea water of the same chlorinity. Bicarbonate and sulphate are high and are present in part as sodium salts, the origin of which is not obvious; unless it be by base exchange between dissolved sodium chloride and limestone rocks. *p*H determined after the samples had stood 18 days was as high as 9·0 in the water from Wyken Slough and 8·8 in that from the Droitwich river. In a sample taken from the Droitwich river on December 8 1938, after a period of heavy rainfall, *p*H had fallen to 7·9 but otherwise the water resembled the August sample somewhat diluted. It is evident that these waters provide an unusual ecological environment and deserve a more systematic investigation than has here been possible. Excess base, *p*H and chloride are expecially worthy of further study.

The water from the Avon at Tewkesbury, in which a few specimens of *G. tigrinus* were found, although essentially a normal hard water contains sufficient sodium chloride to suggest some admixture of saline water of the Droitwich type. Nearly 10 % of the "total solids" remained unaccounted for. Part may be attributed to organic matter in which the water was rich. Since the Avon water was not the main subject of study, the cause of the deficiency was not further sought.

TABLE I.

COMPOSITION IN MILLI-EQUIVALENTS PER LITRE

	Droitwich Spa*	Droitwich River		Wyken Slough	River Avon Tewkesbury
		Aug. 1938	Dec. 1938	Aug. 1938	Aug. 1938
Na^+ (calc.)	5247·4	36·46	—	29·40	2·37
Ca^{++}	68·3	10·22	—	2·22	5·88
Mg^{++}	10·9	6·66	—	3·99	3·92
Total cations	5326·6	53·34	—	35·61	12·17
Cl'	5232·7	41·63	28·89	18·64	2·10
SO_4''	93·5	8·10	—	7·55	4·35
HCO_3'	0·4	3·32	3·02	8·79	5·72
CO_3''	—	0·29	0·00	0·63	0·00
Total anions	5326·6	53·34	—	35·61	12·17
*p*H	—	8·8	7·9	9·0	—

PERCENTAGE COMPOSITION OF TOTAL SOLIDS DRIED AT 180° C.

	Droitwich River		Wyken Slough	River Avon Tewkesbury
	Aug. 1938	Dec. 1938	Aug. 1938	Aug. 1938
Na (calc.)	26·2	—	32·4	7·0
Ca	6·4	—	2·1	15·0
Mg	2·5	—	2·3	6·1
Cl	46·0	47·1	31·0	9·5
SO_4	12·1	—	17·0	26·6
CO_3 (including HCO_3)	3·6	8·46	14·1	21·9
H_2O (in $MgSO_4.H_2O$)	1·9	—	1·7	4·5
	98·7	—	100·6	90·6
Total solids at 180° C. (g./l.)	3·202	2·174	2·135	0·785

* Analysis by H. B. Salt, *The Natural Brine Baths of Droitwich Spa and the Surroundings*. Whately, Droitwich. (No date).

EXPLANATION OF PLATES

PLATE IV

Gammarus tigrinus n.sp. × 12. The figure was drawn from a freshly captured male, from Droitwich river, November 1938. It shows the colour pattern in life. The pale green colour of the body is represented here by light grey; the bright yellow bands on the posterior margins of the body-segments by clear spaces; and the deep indigo blue of the stripes, bars and patches by the dark tint. The red is as it appears in the living animal. Most of the sensory hairs on the appendages have been omitted, for the sake of clearness of outline.

PLATE V

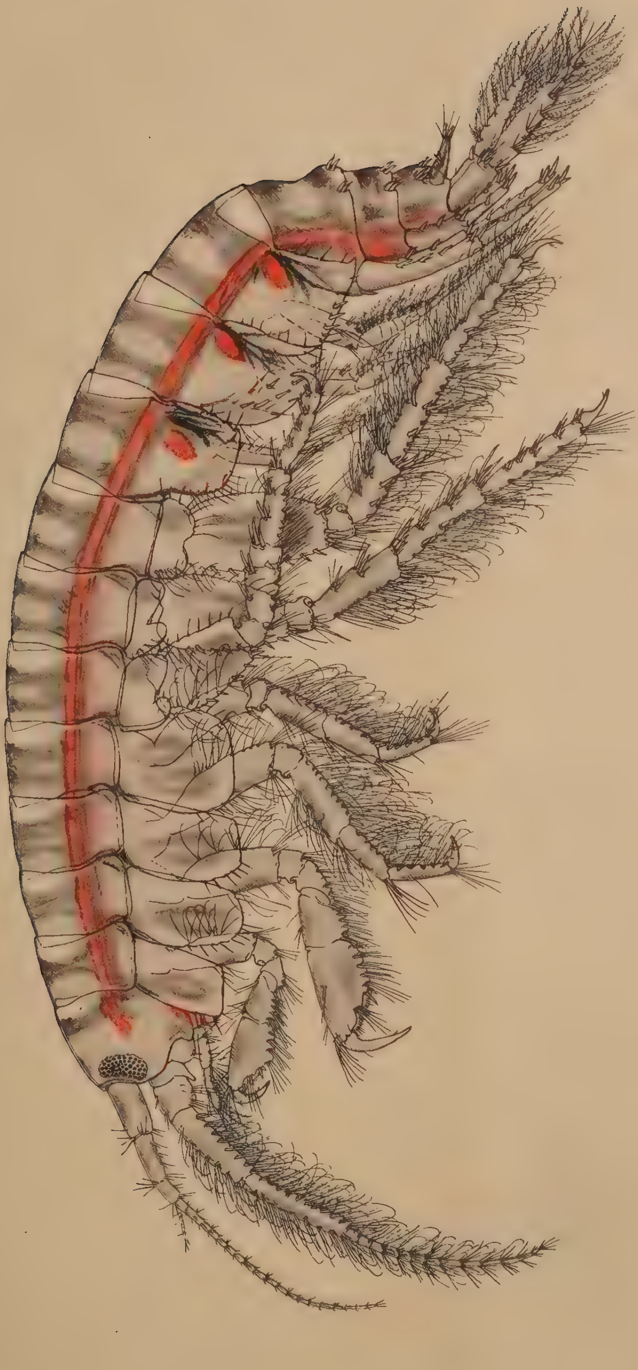
The figures are drawn from one specimen, a male, left side. × 28, unless otherwise stated

Fig. 1. Antenna 1.
Fig. 2. Calceolus from under surface of primary flagellum, antenna 1. × 200.
Fig. 3. Antenna 2.
Fig. 4. Antenna 2, ♀. Left side.
Fig. 5. Gnathopod 1.
Fig. 6. Palmar angle, under-surface, left hand, gnathopod 1, from specimen figured, showing the groups of spines between which the claw closes down. × 57.
Fig. 7. Gnathopod 2, with gill outlined.
Fig. 8. Palmar angle, under surface, left hand, gnathopod 2. × 57.
Fig. 9. Hand of gnathopod 1. ♀.
Fig. 10. Hand of gnathopod 2, ♀, same specimen; gill not shown, brood-plate figured separately.
Fig. 11. Incubatory lamella, or brood-plate from gnathopod 2.
*Fig. 12. Peraeopod 1, with gill attached.
*Fig. 13. Peraeopod 2.

PLATE VI

*Fig. 14. Peraeopod 3.
Fig. 15. Stiletto spine from second joint, peraeopod 3. × 200.
*Fig. 16. Peraeopod 4.
*Fig. 17. Peraeopod 5.
Fig. 18. Pleon-segment 1 with pleopod.
Fig. 19. Pleon-segment 2, epimeron.
Fig. 20. Cleft spine, from basal joint of inner ramus, pleopod 3. × 200.
Fig. 21. Coupling-spines from the peduncle of pleopod 3. × 200.
Fig. 22. Pleon segment 3, epimeron.
Fig. 23. First uropod.
Fig. 24. Second uropod.
Fig. 25. Third uropod. (The proportions of the rami are unusual, the inner ramus being shorter than normal, probably regenerating.)
Fig. 26. Telson.
Fig. 27. Cuticle, showing the spinules covering the body, and the inset sensory processes, from the dorsum of pleon segment 4. × 200.

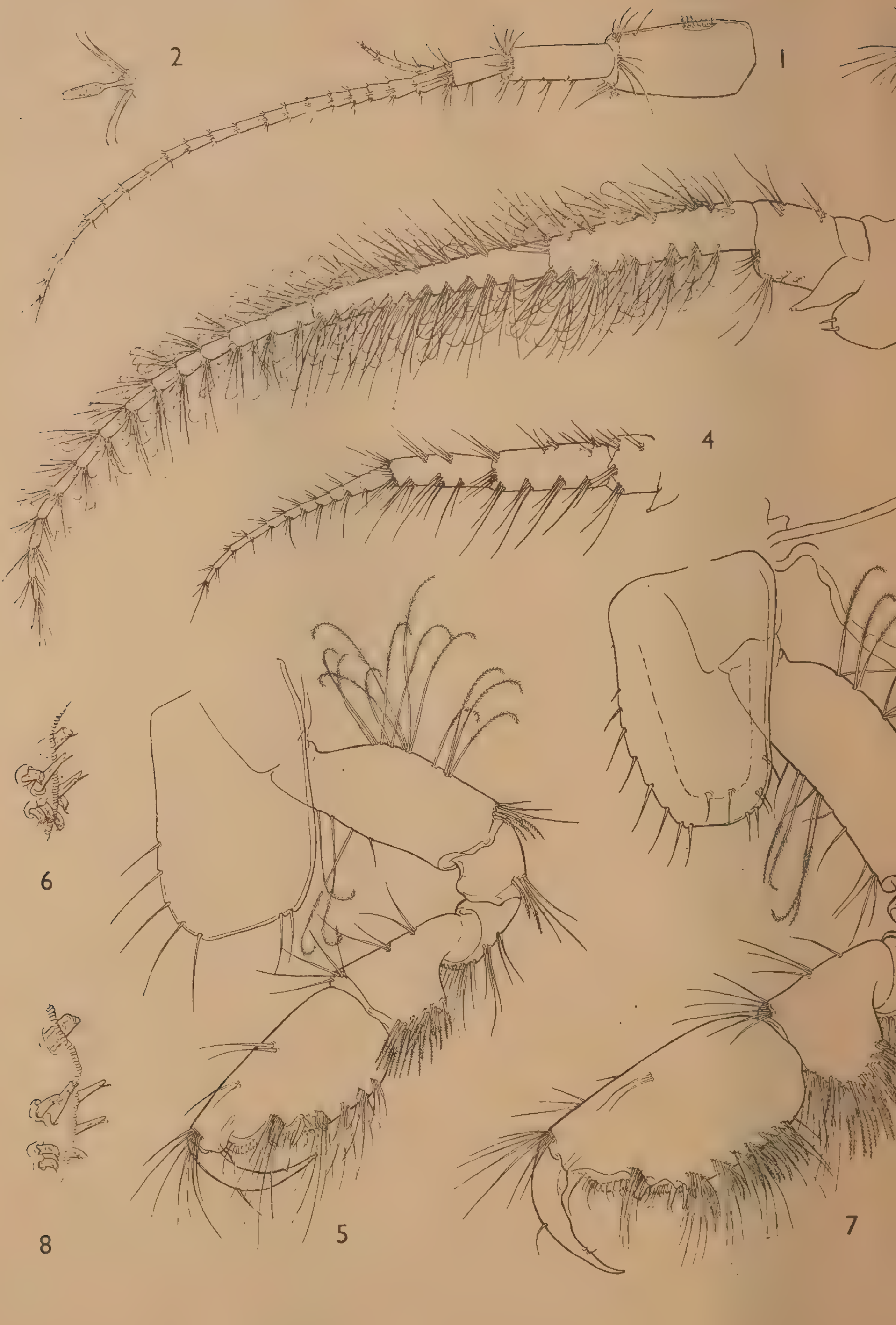
* In these figures it has not been possible to represent the full number of the sensory hairs.



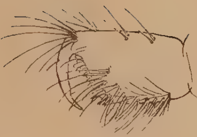
GAMMARUS TIGRINUS n. sp.

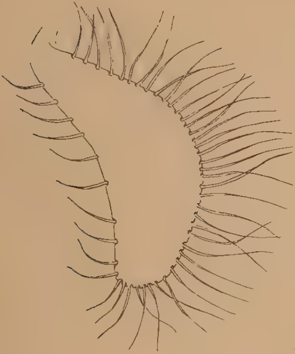
John Bale Sons & Curnow, Ltd London.

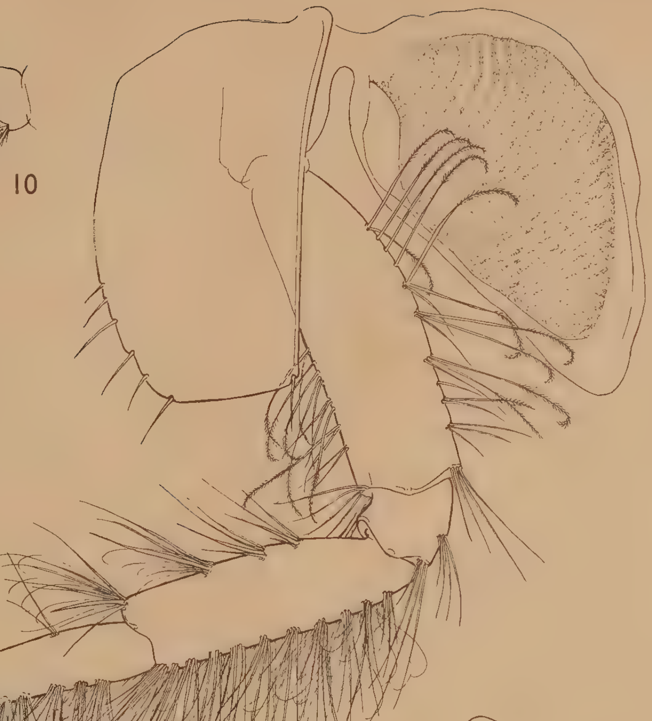
E.W.S. del.

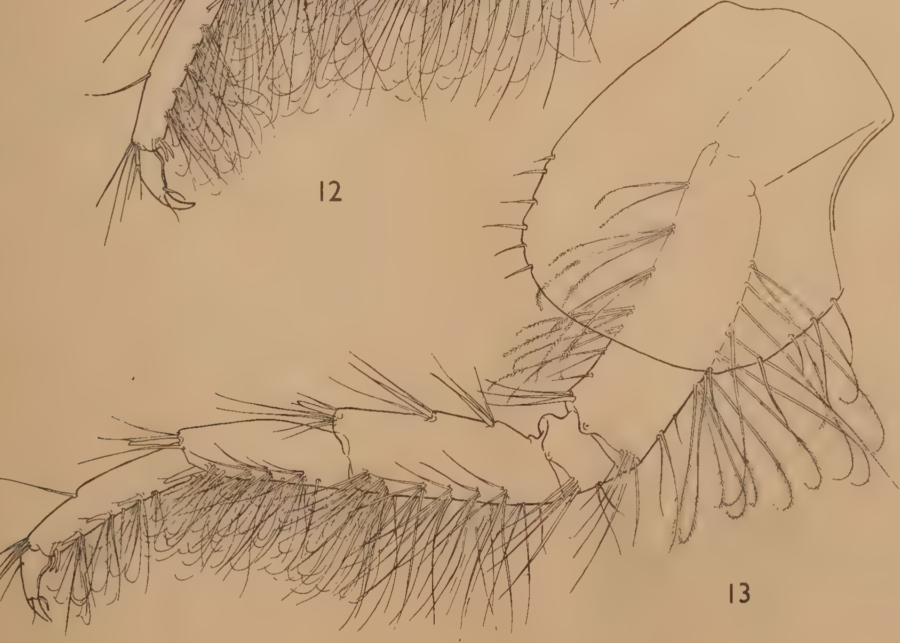


9


10


11


12


13

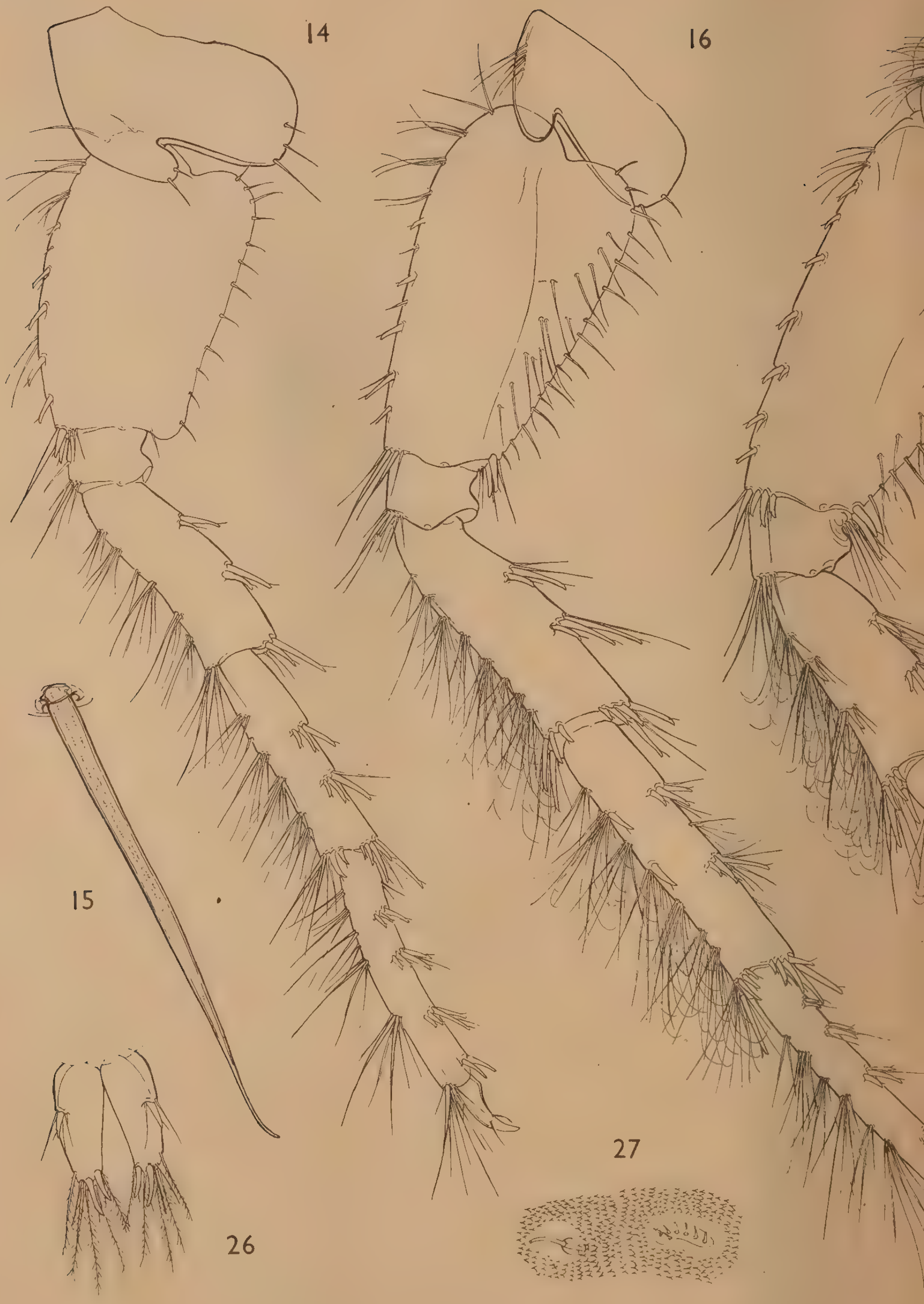
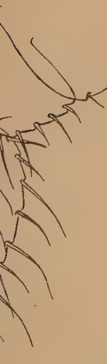
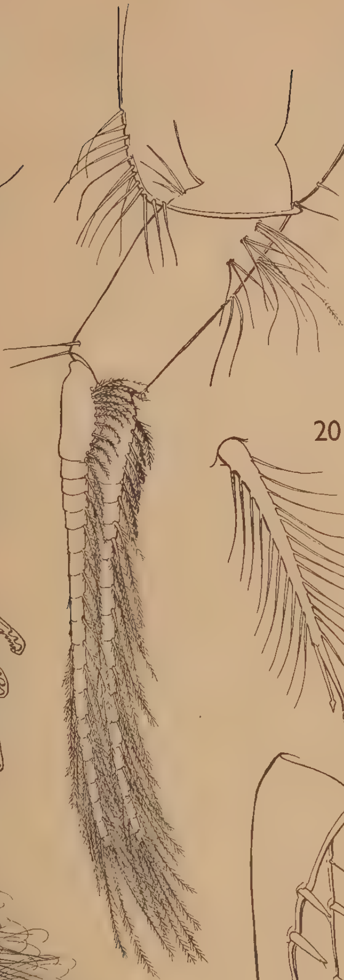
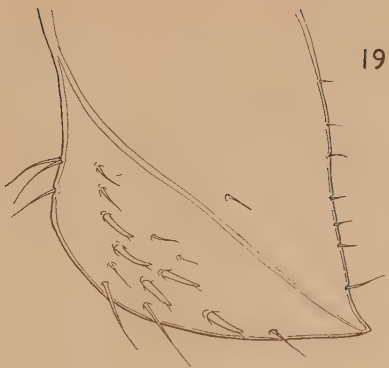
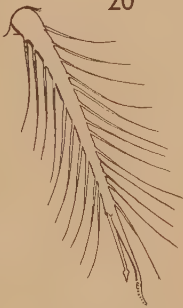


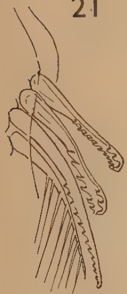
PLATE VI

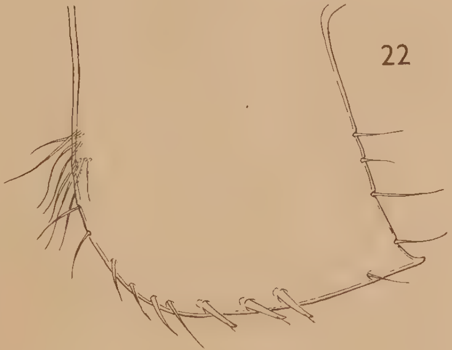

17

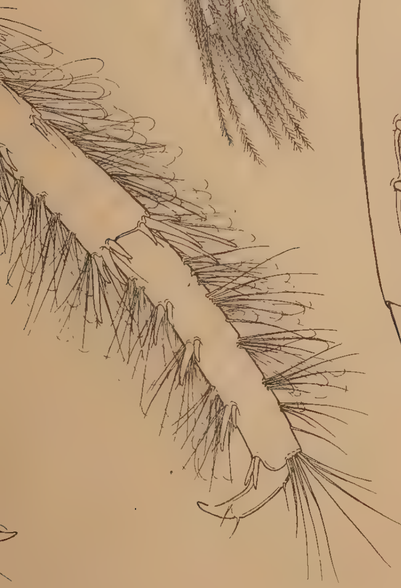

18

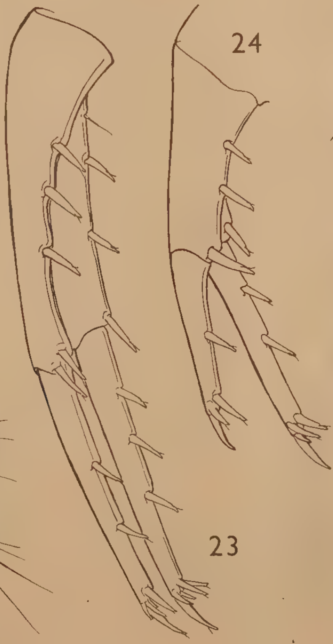

19


20

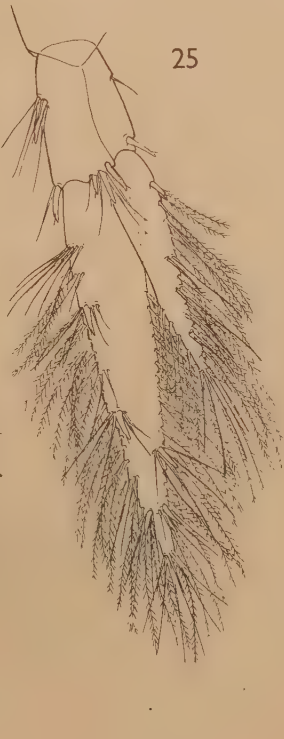

21


22




24

23


25

STUDIES IN THE MARKET SPONGES
I. GROWTH FROM THE PLANTED CUTTING

By L. R. Crawshay, M.A.
Lately Research Officer, Sponge Fishery Investigations

(Text-fig. 1)

CONTENTS

PAGE

Historical:

Early knowledge . . . 553
F. Cavolini, 1785, 1790 . . . 554
O. Schmidt, 1862–4 . . . 555
G. Buccich, 1864–72 . . . 556
Early planting in Florida, 1879–98 . . . 558
H. F. Moore, 1901–5 . . . 558

Growth from the cutting:

Localities and methods, 1921–34 . . . 560
Reconstruction, basal growth, and rounding . . . 560
Food supply . . . 564
Limitation and increase of growth . . . 564
Growth rate . . . 566
Size of cuttings . . . 568
Cuttings from large sponges . . . 570
Breeding process in cuttings . . . 570
Duration of life . . . 571
Summary . . . 572
References . . . 574

HISTORICAL

Early Knowledge

Reconstructive growth in sponges, in its broad sense at least, was probably well known to the early Greeks. A passage is quoted by Oscar Schmidt (1862) from a translated text of Aristotle's *Historia*, in which, referring especially to his second sponge, πυκνός, the statement occurs: "Si autem abrumpantur, ex eo quod relictum est, renascuntur et complentur." This is omitted in D'Arcy Thompson's translation (1910), though in another place (548*b*, 15) a revised passage appears in nearly similar words: "but, if the sponge be broken off, it grows again from the remaining stump and the place is soon as well covered as before". It is, in any case, scarcely credible that a fact so generally known to sponge fishermen of the present day as the repair and renewed growth of a sponge from its torn attached remnant was not similarly known to fishermen of the distant past.

F. Cavolini, 1785, 1790

It remained for Cavolini (1785, 1853), in the years 1785 and 1790, first to throw important light on this subject, through a number of experiments made by him with living sponges. In these experiments, which he carried out in certain sea caves at Naples, Cavolini was not concerned with any general economic question, but primarily with confirming his belief in the animal nature of sponges, as against the assertion of a recent observer that they were vegetables. The question was especially concerned with contraction of sponges when touched in the sea, as observed by the ancients, apparently here referring to Aristotle (1910, 548*b*, 10), and as confirmed by statements of the divers. Of the three sponges named, as chiefly used by him, the "Spugna officinale del Linneo" may possibly have been a form of the *S. mollissima* of O. Schmidt, though this is doubtful; the "Spugna carnose" was certainly a Hircinian; of the third, the "Spugna detta alcionio foraminoso dall' Imperato", the identity is obscure.

Failure of preliminary rough tests with an iron hook, on sponges growing on the sea bottom, to show the distinct body contraction which he expected, led to his hooking them from the bottom, and redepositing them in the sea for observation. The receptacles which he used for this purpose were of red pottery; not, as stated by Marenzeller (1878), ordinary vessels, but small bells (campanelle) made of this substance, used by boys in their play and apparently similar in form to sheep bells. Inside these, suitably small sponges of 2–3 in. in diameter were placed, pierced and threaded through with a piece of cord, the ends of which were secured through the two holes at the inner end of the bell, where the clapper (battoccio) is normally fastened. The bells with their contents were then lowered into the sea and left for different periods—at first for 12 days—after which, when again raised, it was found that besides healing of the torn surfaces the sponges had made spreading attachment to the face of the bells, and in one case the author states that two were so closely grown together that he could not separate them.

Of the later observations, extending from May to August 1790, the ultimately published account (Cavolini, 1853) is rather fragmentary and lacking in continuity, being mainly, as it seems, a collection of incomplete records made by Cavolini covering this period. In these experiments, sponges were also fastened externally to the bells, some being much incised, or completely cut asunder into as many as four pieces, though whether any were planted as separate fragments is not clearly recorded. The purpose of this cutting was, in fact, further to observe the process of repair, which had previously been noted in the healing of injuries caused by the hooks, and especially injury of the torn base of the sponge removed from its natural attachment; full evidence of this repair appearing in his results. A statement in the earlier memoir (Cavolini, 1785), of the author's confirmation of the assertion by the ancients that the sponge uprooted from the rock repairs itself from the root that remains, is apparently a direct reference to the passage attributed to Aristotle by Schmidt (p. 553).

It should here be mentioned that a remark by Vosmaer (1887, p. 29), where alluding to Cavolini having maintained the animal nature of many sponges, "obwohl er meint, dass die von früheren Autoren ausgesprochene Ansicht in Betreff der Contractilität der Schwämme eine irrige sei", is incorrect. As in the care of his material, Cavolini's statements are often marked by extreme caution. But that his observations confirmed the presence of such contractility is made clear by him from an early point in his experiments; although the process is so slight and gradual that, like the movements of the hands of a clock, bodily contraction is not easy to discern. Similarly later: "Risulta da ciò che la spugna sia degli animali lo più semplice: giacchè il suo muscolare è come una cellulare diradata, come una gelatina; che anzi questa gelatina viene inceppata tra quello ramosissimo semicorneo scheletro: i suoi moti provenienti dalla sensazione, sono debolissimi, e siccome più diradato è questo muscolare, cosi il sentimento minora, come accade nel citato alcionio d' Imperato" (Cavolini, 1785, p. 271).

O. Schmidt, 1862–4

About or shortly before the year 1862, Oscar Schmidt first drew attention to the economic possibilities of sponge culture offered by the planting of cuttings in an article contributed by him to the *Wiener Zeitung*; as a result he was invited soon afterwards by the Austrian Government to undertake experiments in this direction with the assurance of all necessary assistance. Schmidt (1862, p. 22) had stated that it was "known" that if an entirely fresh sponge was cut into suitable small pieces, and if these were replaced in the sea, they would grow and develop to complete individuals; later alluding (Schmidt, 1878, p. 534) to the experience of naturalists in this connexion, and especially of Lieberkühn. If he was aware of the work of Cavolini, he makes no direct allusion to it. Marenzeller (1878), in his later review of the experiments of Schmidt and Buccich, seems to infer that he was not aware of it, alluding only incidentally to Cavolini's observations in a footnote, and remarking that these had later fallen into oblivion. Had it been otherwise it would seem strange that Schmidt did not at the outset perceive in the simple device of Cavolini, or more particularly in his use of pottery, a more promising medium of attachment than that of wood, which was destined greatly to increase the difficulties encountered by him and by Buccich.

Schmidt's (1864) preliminary experiments were carried out in the spring of 1863, at Zlarin, and in the Bay of Socolizza of Lesina Island, in the Adriatic. The selected sponges were small, namely, of 2–2½ in. in diameter, these being cut into from four to seven pieces. The fragments were then fastened by smal wooden pegs to the bottom of wooden cases bored, in the sides and cover, with numerous holes of ¾–1 in. in diameter, and so that on a surface of 2 sq. ft.

from twelve to twenty such pieces were placed. Three such containers, with their cuttings, were then loaded with stones and sunk in the sea in a depth of 8–10 ft. Examination of the contents after 4 weeks showed that while some of the cuttings had suffered harm from deposited mud, most of them appeared to be in healthy condition. Later, however, at 3 months from planting conditions were found to be far otherwise, comparatively few of the cuttings surviving. Losses were largely attributed to accumulating mud, though at the same time much harm had been caused by interference with the experiments, and removal of the material by fishermen.

Prior to this, Schmidt had observed that certain details of method needed correction and improvement. A substitute, for example, was required for the closed cases which were detrimental. Change also was needed in the method of attachment of the cuttings to which injury had occurred in the region of the wooden pins. On the whole he was confident that the main project in view was economically practicable. He did not perceive that in cuttings of so small a size a great additional strain was placed on the material in any conditions not wholly favourable to healthy growth.

G. Buccich, 1864–72

In May of the following year, 1864, it seems that the charge of the work was passed over wholly to Gregor Buccich, a telegraph operator at Lesina, who received for some time an appropriation from the Ministry of Agriculture in Vienna, and continued the experiments for some 6 years or more, the station being finally closed in 1872. Details of the work and its results are described by Marenzeller (1878), who had access to all official reports, including especially that of Buccich on the whole subject, which forms the basis of Marenzeller's account.

From the latter it appears that the work was seriously obstructed throughout by continued disturbance, both accidentally and often intentionally, on the part of the local fishermen, and through a generally hostile attitude towards such innovations; and, in spite of the repeated protests made by Buccich, its continuance became, through this cause, impossible. In a brief allusion to the circumstances by Schmidt himself (1878, p. 535), shortly before the publication of Marenzeller's report, ultimate failure of the experiments was attributed to this cause, and secondarily to the destruction by *Teredo* of the woodwork employed. Apart from these facts he expressed no doubt concerning the satisfactory progress of the material itself, nor did he change his views regarding the economic possibilities of the general project.

Buccich's methods seem to have varied comparatively little from those previously used by Schmidt. Perforated wooden containers, in one form or another, continued to be used, the cuttings being fastened by wooden pins, which were ultimately secured in lengths of bamboo fixed in the containers. The latter were then ballasted with stones, and sunk to a depth of 5–7 m.

Alternatively, fastening of the cuttings directly to flagstones was tried, but later abandoned through harmful results, attributed to accumulations of bottom deposit. Here also, as elsewhere, allusion is made to the supposed harmful effects of direct light on the cuttings. This has at no time been borne out within my personal experience, even in the full tropical sunlight of the West Indies, or in a small number of cuttings, planted in about 5 fathoms, and observed for a few weeks, during a stay in Cyprus in 1929.

Sponges collected preparatory to planting were fastened inside a sort of fish carrier; and were later cut, with the minimum of delay, to a size stated as about 26 mm. square. They were thus presumably about 1 cu. in. in volume, and nearly the same size as in Schmidt's first experiments. It will later be shown that a cubic inch would represent about one-tenth part only of the approximate volume of the standard-sized cutting latterly adopted in the West Indian planting.

Details of growth and general progress, obtainable from the report, are very limited, and especially, as stated by Marenzeller, owing to the disturbance of any continued observations. If the statement of Buccich, that in the first year a cutting grew to two or three times its original size, had reference to volume, this would represent a fair to good rate of progress. That he should have found, as stated, less growth in the second and third years than in the first and fourth years, is well conceivable only if in the middle period a comparatively reduced food supply occurred, as in some years may happen, and perhaps through exceptional shortage in rainfall.

The estimate by Buccich, of 7 years as the approximate period required for a cutting to reach marketable size, does not necessarily indicate a slow rate of growth, but is consistent with the very small size of the cuttings as planted. From Schmidt's own more definite statements concerning the size of sponges used, and the number of cuttings made from them, the average cutting volume appears as about 1·1 cu. in. Regarding this as equivalent to a sphere of 1·28 in. in diameter, and, as against the "two or three times" increase in the first year, allowing an average annual volume growth factor of 2·0 for the whole period, in 7 years an average diameter of about 6·5 in. would be attained—or, in the more probable depressed form, a horizontal diameter exceeding this—which might reasonably be regarded as of "marketable" size. Had the cuttings been even six times the estimated volume, which again would be much below the optimum, they would have been capable, with the same average annual factor of 2·0, of reaching the same size of 6·5 in. in average diameter in about 4·4 years.

The division of sponges into very small cuttings (prompted mainly, no doubt, by the mistaken idea of economy) has been an almost invariable tendency at the outset of planting and has certainly been one of the chief factors which have retarded progress in sponge culture. There seems, however, in the present experiments, to have been much lack of discretion in the handling of the sponges between collection and planting. Reference is made to the length of time during which sponges may with safety be left out of water, or on dry land, in winter and in summer, the time sometimes extending to hours. If, as too probably, this means that such unnecessary exposure of the sponges was often allowed to occur, there can be no doubt that much of the material must have suffered harm. Eighty years previously, Cavolini had followed the extreme and safer course of not allowing his sponges to pass through the air at all.

Early Planting in Florida, 1879–98

After the experiments at Lesina, certain attempts at economic sponge culture were made on the coast of Florida, and the results are referred to by Rathbun (1887) and more especially by Moore (1908). These were, first a small experiment in about 1879 by Fogarty, a buyer in Key West, with cuttings attached to stakes and wires; which was not carried to a conclusion. Later, and for some years following, Monroe experimented at Biscayne Bay with cuttings fastened to staves, stakes, etc., but without any definite success. In a more extensive experiment, about 1897–8 by Dr Harris at Sugar Loaf Key, with some thousands of cuttings attached to galvanized wire, corrosion and breaking of the wire led to detachment and loss of the sponges with high mortality. None of these experiments yielded any serviceable data.

H. F. Moore, 1901–5

Dr H. F. Moore was commissioned by the U.S. Bureau of Fisheries in 1901 to carry out experiments in different methods of improving the Florida fishery, and his results concerning sponge culture, extending over about 4 years, are fully described in his report (1908). Here it is only necessary to mention certain points in his work, which resulted in a very great advance in our knowledge of the subject. In methods chiefly needing attention for successful planting, a question of primary importance was the selection of a suitable medium of attachment for the planted cuttings. Ultimately, after many trials of different substances and in different forms, Moore was led to adopt the concrete disc, which, except for reduction of the original size, about 10 in. in diameter, and perhaps some modification in form, is unlikely to be surpassed for practical purposes.

For attachment to the disc, except when a short wire spindle vertically piercing the cutting was used, a piece of small-gauge aluminium wire was passed through the cutting and through a hole in the disc on either side of it, the ends being twisted together below. In this manner the cutting was secured in position until able to form its own attachment to the disc. The size of the cuttings planted was at first small; subsequently, however, it was increased to about $1\frac{1}{2}$ by $2\frac{1}{2}$ by 3 in., or with a volume stated to be about 8–10 cu. in., the latter being roughly the same as that adopted for cuttings in the West Indian experiments.

Rate of growth in the planted cuttings was found to vary appreciably in different localities. The exact details are somewhat difficult to interpret, owing to the fact that Moore expresses growth mainly in terms of an annual increase of diameter, quoted as a single quantity only. If, as is to be presumed, this was an average of three dimensions, any such increase in a massive sponge must necessarily depend much on the volume of the latter, and itself increase annually with regular growth. In two grounds selected for comparison, Sugar Loaf Sound and Anclote Key, this annual diameter increase was found to be about 0·8 in. in the former, and about 1 in. in the latter. It was accordingly deduced that growth was slower in the one locality than in the other, and Moore was led to infer that at Sugar Loaf Sound the observations indicated the presence of a dwarfed stock of slower growth. He thought that this dwarfing resulted from the intensive fishing in the shallow and more accessible waters of the Sound and from the constant removal of the larger sponges. It is conceivable that in the course of time such a result might ultimately come to pass; but it is difficult to believe that it could happen in the comparatively short period of some 50 years, since the Florida fishery first attracted commercial interest, i.e. about 1852 (Rathbun, 1887, p. 830).

The observed growth rates are, however, shown graphically in a series of curves for each of the two grounds in question, indicating the volume increase recorded periodically for different series of cuttings. Examination of these curves does not clearly bear out the conclusion that there is an appreciable difference in growth rate on the two grounds. While for Sugar Loaf Sound a factor as low as 1·76 for increase in volume occurs for one short-period series covering 12 months, the average annual factor for the three series together amounts to 1·99. As against this, the corresponding three series for Anclote Key, though more nearly uniform with factors between 2·03 and 2·16, show an average of 2·11. Also, as between the two long-period series, covering 2·9 years for Sugar Loaf Sound, and 4·0 years for Anklote Key, the difference in average for the whole period is again comparatively slight, the figures being 1·99 (the same as the average for this ground) and 2·16, respectively. It may here be mentioned that in the light of the West Indian observations an annual growth factor of 2·0 is generally to be regarded as a fair rate, though not a high one; if maintained from year to year it gives no cause to doubt the generally healthy progress of the growing material.

Moore concluded that a greater aggregate volume is ultimately attained by a greater number of cuttings: or as definitely suggested, by fifty as against twenty cuttings made from the same sponge. It is possible that this view was reached owing to the inadequate data available during the limited period of his observations; and it may also be due to incompleteness of results, through interference with the experiments, of which he complains, and other causes of material loss. Within my personal experience there is no evidence to support this view, for, assuming uniformly favourable conditions for growth, the rate of volume increase, though varying between different individual sponges, is approximately the same for a large cutting as for a small one, made from the same sponge. Apart from positively adverse conditions decrease in the growth factor only appears with approach in size to the maximum volume which the feeding capacity of the sponge can sustain, and this again varies much between different individuals.

GROWTH FROM THE CUTTING

Localities and Methods, 1921–34

This section of the paper, concerning the general subject of growth from the cutting, is based on observations and experience acquired during the course of the Sponge Fishery Investigations, which were carried out on behalf of the Colonial Office and extended over several years. The data were largely obtained on the coastal grounds of the Island of Abaco, in the northern part of the Bahamas, between the years 1921 and 1928; but included also are the results of numerous planting experiments carried out in the Lagoon of Turneffe, British Honduras, between 1926 and 1934.

In the Bahamas, sponges collected from different and often distant grounds were carried in boats fitted with flooded wells kept in communication with the sea, and thus conveyed to the experimental depot ground, closely adjacent to the Laboratory, where they were deposited, either for observation as complete sponges, or for subsequent division into cuttings. In British Honduras similar methods were followed, but as the station was located on a reef it had not the facilities of an adjacent depot; observation of the material was made by periodic visits to the different planting centres, extending over a large area within the lagoon, from within which all sponges were obtained.

For purposes of basal support, concrete discs were used throughout from an early date. The size of these ranged from 3½ to 10 in. in diameter; the latter was used infrequently and for special purposes only, the disc chiefly used during the later part of the work being 4½ in. in diameter at the upper surface. Except in certain grouping experiments, all discs were numbered by means of a series of short cuts made with a hacksaw, proceeding from a zero point on the upper surface and arranged on a decimal system around the different faces and edges of the disc. These marks were thus indelible; they could be extended to high numbers and with their help the progress of the cutting could be recorded over an indefinite period.

Reconstruction, Basal Growth and Rounding

Assuming the presence of favourable conditions of location and the important essential of careful handling of the material, fragmentation, carried out by the clean cutting of a market sponge, is followed in a very short period, commencing almost at once, by a lengthy process of general reconstruction, as required to equip the cutting for independent existence and self-maintenance. If all things are favourable the loss in volume directly due to cutting is, or should be, practically negligible.

It may be noted here that a normal and healthy sponge has certain requirements in which a cutting is at first partially or wholly deficient. These include the complete investment of the whole outer surface with a covering pellicle, accompanied in parts, where much exposed to the sunlight, by a protecting zone of densely pigmented cells, and normally—though not strictly essential—some basis of attachment. In addition the canal system contained within the severed fragment must be modified to suit the sponge to a separate existence.

Though a cutting may be orientated in any position, and, as mentioned by Moore, successful growth may be effected by a fragment from the interior of the sponge without any part of the dermal surface, absence of the latter is liable at least to retard progress in early growth, if not to give occasion to higher mortality. On this point the results of the experiments have led to the conclusion that the optimum conditions in planting are provided by retaining in the fragment a portion of the original dermal surface, and securing the latter downwards, against the concrete planting disc, or other base of attachment. It follows therefore that, in this position, the change involves considerable readjustment of the canal system, for the surviving remnant of the pore-bearing surface has now to be closed off to form the attaching base of the new sponge.

In the newly cut fragment (Fig. 1) it is questionable whether any one or other of these processes has a prior call. All appear to proceed simultaneously. Healing—the formation of a delicate covering on the cut surfaces—is a matter of a few hours only. Concurrently with this, closure of the larger surface apertures—no longer to function as previously, or only very partially so, in the new canal system—is more gradual, and in accordance with their size may occupy a day or two for purposes of preliminary completion. In this the process appears to be much more a matter of upgrowth and closing from within and below than of covering in at the extreme surface. The importance of this is evident in cases of local subsurface injury, where, if the injured part becomes enclosed within the body of the sponge, need may arise for the complete walling off of an interior damaged and macerating region. Such a space, especially if large, is liable not to be reoccupied, but to remain a closed cavity containing at length only the remnants of the dead skeleton. Otherwise, if close to the surface, the injured region will in due course be sloughed off, and the space will probably be refilled ultimately by new growth from below.

Simultaneously with the new dermal covering a varying number of quite small apertures are left unclosed to form the new oscula.

The number of these, though variable and differing with the characters of the sponge, is usually very small; and in small cuttings at least there may at first be no more than one. The position is also very variable, and probably determined by that point of the new surface where a section of the existing canal system provides the most complete and effective means of communication with the remainder in the adjustment of the new system of circulation. Commonly, around each of these early oscula, a delicate tubular outgrowth is soon extended, and very shortly a strongly working circulation is restored.

Concurrently with this change, pigmentation of the newly cut surfaces proceeds by gradual stages; and if light conditions are strong, becomes appreciably visible to the eye within a few hours. Complete "blackening" of the surface, which is a matter of degree in the massing of increasing numbers of deep brown pigmented cells at and below it, is more gradual, and may occupy a week or two, depending on the intensity of the sunlight. Where screened from the sun, as in certain lower parts of the subsequently growing sponge, pigmentation is much reduced or wholly absent.

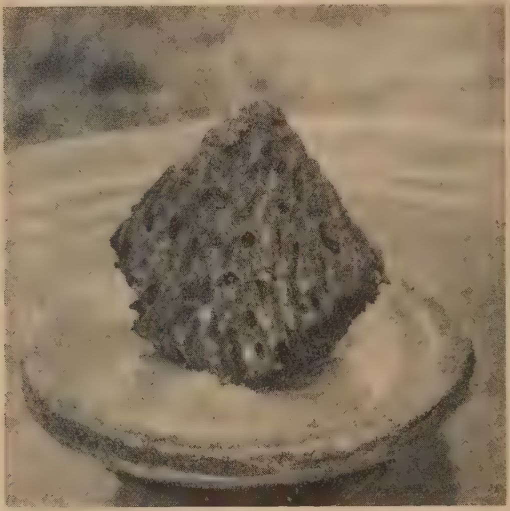


Fig. 1. Newly made cutting from a Wool sponge. The disc is 7 in. in diameter.

Progress in growth and change is necessarily very variable, depending on food supply and other conditions. Where a fixed base of attachment is present, as provided by the concrete disc to which the cutting is firmly secured (see Fig. 1), downward growth from the lower region of the cutting is a prominent feature from an early period; and continues until complete attachment to the disc is effected by the sponge itself. This process is gradual, and may occupy a period ranging from a few weeks to a few months, depending much on circumstances of location. If the position is disturbed, or the cutting insecurely fastened at the outset, attachment may never occur, the base then becoming merely rounded off and strengthened against friction by additional fibres. It should here be explained that it has been customary of late years for certain planters to follow the method adopted by Moore of fastening the cutting by a length of aluminium wire passed through it, and through a hole in the disc. The method adopted in all planting experiments here described has, however, been to secure the cutting firmly by means of a pin, passing through both cutting and disc. This pin is made from the thoroughly dried stalk of palmetto, with a small projecting head at the upper end to prevent lifting of the cutting.

When the basal attachment is completed it is usually followed by a more or less pronounced extension of the base as a thin marginal plate, and it is probable that this process has as much importance for feeding purposes in that region as for general attachment.* After a time the basal marginal extension not infrequently reaches the edge of the planting disc; it will then often pass over the edge, and continue down the side until, with increasing growth, the whole of the disc except the lower surface may become enclosed within the base of the sponge.

As previously stated, the rule adopted almost invariably, from an early period of the work, has been to plant the cutting with its portion of the dermal surface downwards and tangentially against the disc. The exact details of the fate of the original dermal covering of this part of the cutting have not been followed. It seems that, in a healthy sponge, it must be absorbed. In the ultimate basal growth there remains no visible trace of it as distinct from any other part of the original cut fragment, but in section it is usually distinguishable by its darker colour from the new growth around it. The ultimate investment of the disc, or other basis, by the cutting is so complete that in the grown sponge every detail of irregularity in the surface of the object is usually distinctly impressed on the base of the sponge and on the surface of its skeletal network after maceration.

On this subject of basal growth—perhaps more properly, in its origin at least, to be regarded as cell migration—some digression has been made from that of the general growth. Assuming that roundness is a character of the original sponge, a primary object in growth is to restore rotundity of form to a cutting which is at first roughly pyramidal (Fig. 1). This restoration takes place through a gradually increasing convexity of the separate cut faces as a first step, with, later, complete obliteration of the original lines of the cutting. Progress in this direction will vary considerably with location: on grounds where food supply is abundant, and growth rapid, rotundity may be acquired in about 3 or 4 months; on other grounds it may take twice the time, or longer.

Roundness of form, however, in any strict sense of symmetry or regularity, is very far from being an invariable rule among the market sponges, or in any one species of them; and, though the question of form variability cannot conveniently be discussed here, it may be stated that where any marked irregularity of growth occurs in a sponge the features constituting such irregularity will usually be shown in the cutting made from it at an early stage of growth, and independently of roundness as a premier character.

---

* It should perhaps be explained that this basal outgrowth is here regarded simply as an outward extension of the sponge body, and as functioning in continuity with it in all respects. Though not examined in detail, the conditions are apparently similar to those of corresponding basal outgrowths formed by certain Plymouth sponges, while kept under observation in the laboratory, as, for example, in *Esperella*. In these the canal system is continuous, with flagellated chambers extending almost to the extreme limits of the investment.

Food Supply

Rate of progress of a cutting must of necessity depend largely on food supply, the exact nature of which is uncertain. It may, however, be said that, speaking generally, most favourable conditions for growth are usually found in or near to positions subject to regular tidal interchange, combined with the presence of waste organic products carried down from land areas, or otherwise leading to deposits of partially organic mud. It is not improbable that part of the food is derived through ingestion of the finer particles of waste organic matter itself; but the fact that some of the most favourable situations are far removed from land, and chiefly characterized by heavy deposits of extremely fine calcareous mud—produced, as ascertained by Drew (1914), by denitrifying bacteria—suggests that certain bacteria form in themselves the chief source of supply.

Resting in, and largely covered by this mud, commonly at many miles from land, the sponges thrive and grow rapidly, attaining to the largest sizes reached in the Bahamas, and they often retain remarkable regularity and massiveness of form with their increasing growth. The intensity of the bacteria associated with this mud, chiefly *B. calcis*, is well shown in the fact that, at 3 miles out from the shore from the western end of the Southern Bight of Andros, Drew (1914, p. 42) estimated that there were 35,000 bacteria in each c.c. of surface water and 160,000,000 per c.c. in surface samples of the mud. He notes that the last figure may be underestimated owing to settlement of bacteria during the preparation of his cultures.

Limitation and Increase of Growth

In the absence of directly unhealthy factors life may continue in the cutting, even for some years, under conditions of food-shortage; but growth is much retarded or absent, and there may be an actual decrease in the living volume. In such conditions the existing resources of the individual appear to be primarily employed for purposes of attachment, possibly including the quest for food supply through the medium of the basal extension (p. 563), and secondarily for gradual reconstruction of the natural form. In conditions of bare maintenance this may involve some withdrawal from parts of the outer and upper surface areas, ridges and other prominences especially being vacated, and the retraction at times extending over parts of the cut surface to a depth of perhaps $\frac{1}{2}$ cm. or more. Here, the new surface seals itself over, and the vacated skeleton endings shortly die and, after a month or more, slough off, leaving the new dermal surface wholly bare. In extreme cases of serious partial injury, such as possibly occur through temporary conditions of pollution, so long as it does not extend to the entire cutting, an unharmed portion may still effect recovery by walling itself off from the remainder, and in due course forming a completely rounded and separate small unit, perhaps not exceeding about 2–3 cm. in diameter.

In the normal course progress towards completion of the natural form of the original stock will continue, as stated, through rounding of the surface, with gradual obliteration of the original lines of the cutting, and (if rotundity is a character of the sponge) until complete rotundity is reached. The positions of the dominant oscula will, in the meanwhile, be adjusted to the form, and be mainly confined to the upper surface, though in some sponges these may be partly lateral. The attainment of this stage may be slow, extending over a year or more, or, on the other hand, it may occupy only a few months.

Examples in earlier experiments of completely formed small sponges of no more than 6 or 7 cm. in diameter after some 3 to 4 years from planting, appeared at first to support a prior view that growth and the life period are limited by the age of the stock from which the cutting is made. Subsequent observations, however, have not borne out this view; and, as far as is yet known, the possibilities of growth are unlimited by the age factor alone. With the passage of years a sponge grows to exceed its optimum volume in relation to its individual feeding capacity, and the available food supply around it. As with increase in volume the food shortage becomes relatively greater, maintenance of the individual as a complete whole becomes more difficult, and repair of local injuries becomes less complete. Parasitism and overgrowth also cause increasing interference with ingoing currents and excretion; and while modification of form, in adaptation to need, or often partial withdrawal from outlying parts of the skeleton, may prolong life for several years, ultimate decline and death seems rather attributable to uncontrolled growth than directly to loss of cell vitality with age. This view is in general agreement with the conclusions of Bidder (1932) regarding growth and death in sponges of this group.*

Where conditions are favourable to steady growth, increase in the cutting may range from doubling to trebling its volume, or occasionally more, in the year. Speaking generally, though different species vary in this respect, an annual growth factor of less than 2 is rather low, and suggestive of some deficiency, not necessarily harmful, in the local conditions. A factor of 2 may be regarded as fair, or a fair average, while 2·5 indicates a good rate of growth, and from the point of view of the planter is perhaps the most reliable. Increase showing an annual factor of 3 or more is high, and usually concurrent with the presence of exceptional accumulations of waste matter, which may at any time lead to disturbance of healthy conditions and harmful results to the

* See also p. 572.

planted material. Conditions such as these may be quite favourable to sponges of investing or creeping habit, as among certain Halichondriae and others; they are, however, disadvantageous or even dangerous to the large and massive market species, easily leading to congestion of the canal system and interference with excretion, with possibly fatal results. If congestion is not extensive and amounts to no more than mechanical stoppage of the canals, it may be remedied by the sponge itself, through isolation and abandonment of the affected region which will later disintegrate and fall away. Two or three of the growing sponges from a series of cuttings in British Honduras were found to be partially dead 3 years after planting, and examination of the material showed that a large part of the incurrent canals, to a depth of 2–3 cm. below the surface, were closely choked with fine mud. It was accordingly decided to cut and replant most of the remaining members of the series, and, with few exceptions, growth in the new cuttings proceeded normally. It is to be observed that the usual method of planting, with the old dermal surface downwards, served in this case to promote recovery.

GROWTH RATE

For observations of growth rate, it is first to be considered that, with certain exceptions, the general form of most market sponges having any definite approach to symmetry, though occasionally spherical, more commonly approximates to that of a depressed spheroid. Hence, while making any necessary correction required in cases of irregularity, estimates of volume are best obtained by the formula

$$V = \tfrac{4}{3}\pi ab^2,$$

where b is half the mean of two horizontal diameters at right angles, and a is half the height. From the volume thus obtained of a sponge before planting, the fractional average for each cutting at the time of planting is known; and while the size of the cut fragments must necessarily vary, and at times considerably so, for estimates of later growth the selection of about five or six of a planted series will usually suffice to give very nearly the true average rate of progress for the whole.

If V = the initial volume at the time of planting, x = the volume reached at a future date, y = the annual factor of increase, then the ratio of increase x/V for 1 year $= y$; for 2 years $= y^2$; and for n years $= y^n$; and generally, for all values, $y^n = x/V$; or, $y = \sqrt[n]{x/V}$; $\log y = \dfrac{\log x/V}{n}$.

Frequently a value other than y is required, as for example the period at which, with V known and y approximately known or assumed, a certain volume x will be attained; or, in the inverse order, with a present volume regarded as x known and y assumed, the approximate age of the sponge is required. As with the growth factor y, n almost invariably involves a fraction, its exact or approximate value being obtainable through transposition of the last formula.

Estimates of progress in terms of the diameter were not ordinarily used for purposes of the experiments. If so required, and taking here, in each case, the average of three dimensions, if d = the original average diameter of a sponge, D = its increased average diameter, p = the annual factor of increase in the average diameter, then similarly, as in the preceding formula for volumes: $p^n = D/d$; or $p = \sqrt[n]{D/d}$, for any value concerned.

And since p is equivalent to the cube root of the volume factor y; if, for example, the latter is 2·0, and sustained for the period, the average diameter of a sponge will thus be doubled in 3 years. Manifestly this cannot continue for very many years; and herein a striking aspect of sponge growth appears, in the capacity at once to resume such rate of increase as here considered, or a higher one, in a fragment severed from a sponge in which any volume increase may have long since ceased.

Actually, the growth rate of a sponge in a given location has been found to vary appreciably over different periods, and short-period observations may at times be misleading. In an early Abaco experiment (E. 6, Velvet), for example, data for the first 8 months were unobtainable through omission to measure the original sponge. For subsequent periods the following estimates of volume increase were obtained for the average of eight cuttings:

Feb. to Jan.	10·9 months	Equivalent annual factor	2·24
Jan. to Dec.	11·7 months	,, ,,	2·30
Dec. to Aug.	7·5 months	,, ,,	2·67
Total period	2½ years	Average annual factor	2·36

For a single cutting, the largest of the series, the increase through the total period showed a nearly similar average annual factor of 2·34. In this, as in the preceding case, the average rate of increase is calculated direct between the original volume and that of the ultimate growth.

In the foregoing example, as was the custom at the period, the cuttings were very small, and though of unknown volume, certainly did not exceed 2·5 cu. in.

The following example may be given of the high growth rate often observed at Turneffe, British Honduras. Fifteen cuttings of a Wool sponge showed after 9½ months an average increase equivalent to an annual factor of 2·94. This rate, however, was not maintained: one cutting, No. 5585, during the succeeding 19 months, May to December, gave an annual factor of 2·14, while in another, No. 5590, for 20½ months, May to January, it was 2·08. No. 5590 was later replanted as eighteen cuttings on a different and distant ground and three of these cuttings, which alone were measured, gave after 18½ months an average annual growth factor of 3·13. If now the average ultimate volume of these three cuttings—nearly 69 cu. in.— be compared with a similar eighteenth fractional part of the original average cutting at the first subdivision, i.e. 1·02 cu. in., it is seen that the average annual factor for the whole period, 4·04 years, from July 1926 to August 1930, is 2·84, or not far short of that found for the whole series at 9½ months. The two grounds are not quite similar, but the example illustrates the potentially high growth factor of the sponge in question, at the commencement of life as a cutting.

Variability in growth rate among different cuttings of the same sponge is necessarily more pronounced where the general growth factor is high. Though probably due to different causes, there is little doubt that it is largely attributable to the different regions of the sponge from which the cuttings were made, and especially as between the base and the upper and distal parts. In the cutting of a sponge, with comparatively rare exceptions, the general aim has been to replant the whole of the sponge, and in so doing to ensure as far as possible uniformity of size in the cuttings. The method employed is first to divide the sponge vertically into nearly equal complete segments, as many as its size allows; then to subdivide each segment transversely or obliquely to the original "polar" axis of the sponge. In the result it follows that certain cuttings are wholly basal, as contrasted with others from the extreme upper region; and it seems that the stronger growth occurs from the former. Though definite data are very incomplete, this view is supported by certain records of distinctly stronger growth in known basal cuttings. Further, in the few cases observed, it is in the lower region of a young sponge that the reproductive bodies first appear, presumably marking the zone of maximum vitality.

In conditions of food shortage growth may be much retarded or even suspended for a long period, but will again be resumed with change to a more favourable location. In an extreme case, in one of the Abaco experiments, a series of cuttings from a Wool sponge, planted in what proved to be an exceptionally unfavourable position, effected complete reconstruction as well-formed little sponges; but up to 30 months from planting no growth was made, and even a distinct reduction in volume had occurred. Survivors were then moved to another position some 150 yards away, in which after 7 months, when the material had to be removed, a pronounced change with renewed growth was observed, showing approximately the equivalent of an annual factor of 1·7 (though exact results were uncertain through incomplete data). In the second position, where many sponges were placed, the growth rate was usually low, rarely reaching an annual factor of 2·0.

Size of Cuttings

The number of cuttings that can be made economically from a sponge, and the size of the individual cutting, are questions of some importance. In similarly favourable conditions, though cuttings may vary to some extent between one another, small cuttings from the same sponge should make approximately the same rate of progress, in proportion to their volume, as large ones. But it is clearly advisable to observe some uniform standard of cutting volume, whether at all times to be closely adhered to or not, to be retained as an approximate basis of reference and comparison, for records of general progress.

During the latter part of the work such a standard was adopted in the form of a spheroid of 3 by 3 in. in horizontal diameter by 2 in. in height, showing an average diameter of 2·67 in. As sufficing for practical purposes, this was then treated as the diameter of a sphere, and was the unit employed in the preparation of a scale for general reference. The following table is given in illustration: the first column showing the number of cuttings to be made from a sponge of the diameter given in the second column.

Cuttings	Sponge av. diam. in.	Cuttings	Sponge av. diam. in.
1	2·7	35	8·7
2	3·4	40	9·1
3	3·8	45	9·5
4	4·2	50	9·8
5	4·6	55	10·1
6	4·8	60	10·4
7	5·1	65	10·7
8	5·3	70	11·0
9	5·5	75	11·3
10	5·7	80	11·5
15	6·6	85	11·7
20	7·2	90	12·0
25	7·8	95	12·2
30	8·3	100	12·4

In certain of the larger sponges, in which the depression of the spheroid may be considerable, an appreciable difference will occur between its average diameter and that of the sphere of equivalent volume. But, since the diameter of the sphere is the smaller, the result, if uncorrected, will only lead to a slight increase in the size of the cuttings above the standard, and this, on the whole, is preferable in the larger sponge.

It is difficult to cut a sponge at once into more than about sixty fragments without much distortion of the ideal and compact form, and this is liable to place undue strain on the material in its reconstructive growth. It is thus advisable first to cut sponges of large size into three or four large fragments, fastening them together with a piece of line; then later, after an interval of a week or two, when the cut surfaces have healed over, to carry out the complete subdivision. This will give greater scope for orientation of the cuttings, and they will be of a better shape, without having one of the newly cut surfaces resting beneath, which is not desirable.

As an example of steady growth, with exceptional uniformity of progress among the several cuttings and a rather high rate of increase over about 2½ years, through the first stage of cutting, mention may here be made of a Wool sponge planted at Turneffe in October 1927. A special point of interest is the exceptional regularity of the sponge itself, with almost perfect symmetry of form, and with its rather numerous cloacae regularly disposed over the upper surface. This sponge, H. 281, had an average diameter of 9·5 in., and was divided into forty-three cuttings. The cuttings were therefore nearly to the standard scale (which would give 45), though made, as it happened, before any standard unit was adopted. In March 1930, one only of the series was missing. The whole of the remainder had made nearly similar and regular growth, though slightly varying in size, and, for a fairly representative series of ten measured examples, the average annual factor, for 29 months, was found to be 2·67. There can be no doubt that the exceptional symmetry of form of the original sponge was largely accountable for the pronounced uniformity of growth and progress appearing in the whole planted series.

Cuttings from Large Sponges

As bearing on the question of continued growth in cuttings made from a large sponge, the following example is deserving of record. At Turneffe there is a large-growing type of Velvet, of not infrequent occurrence, though regrettably now more scarce than in the past through lack of timely protection of the fishery. An example of this type, H. 38, was obtained in July 1926, having an average diameter of 16·7 in. During removal of the sponge to the planting ground a fragment of it, estimated at rather more than one-third, was carried away by the tide and lost. The remainder, estimated as representing a sponge of about 13·9 in. in average diameter, and equivalent to a standard cutting estimate of about 140 cuttings, was planted as a first step as nine large fragments only, variable in size, but on the average about fifteen times the cutting standard in volume.

Growth in these fragments through the first period of 9½ months could not accurately be known, through uncertainty as to the exact proportion of the sponge which they represented. Later, on the same ground, one of them, No. 6037, showed over 19 months, from May 1927 to December 1928, an annual factor of 2·1. In January 1929, another, No. 6040, having an average diameter of 12·25 in., was moved to another ground, where it was divided into four nearly equal quarters, each quarter being planted in a different position as either fifteen or sixteen cuttings. The cuttings were therefore large in size, as against a standard equivalent of 97 for the whole sponge (table, p. 569). Here, in August 1930, about 18 months later, four measured cuttings from each of two of these quarter-series—the other two not being measured—showed through this period an annual growth factor of 2·6 in one and 2·8 in the other; that is to say, at a date 49 months after the first subdivision of the original sponge, which was probably not less than 15 years old when obtained.

Breeding Process in Cuttings

In the absence of any seriously adverse conditions, no interruption or dislocation of the breeding process, as it would normally take place in the original sponge, should occur in the cutting. The only observed example of such interruption occurred among survivors of some 200 cuttings, planted on the Abaco grounds, which suffered great injury from a serious storm in October 1926. The water was driven from the ground where they were planted, and the cuttings were exposed for some hours to the rain. In this case surviving examples of known breeding material either produced no embryos in the following breeding season, or only very few, and none of these, as far as observed, reached complete larval development. In the ordinary course a fragment cut and planted from breeding stock during the breeding season will continue without check and complete the extrusion of its larvae, as in the original sponge; or, if out of the breeding season, it will proceed with the formation of its proportion of the larval brood next to follow, and will liberate them at the proper season. In Fig. 1 the developing embryos appear as whitish patches distributed over the cut surface.

Duration of Life

In other respects, a sponge grown from a cutting becomes a completely independent organism, and may be recut in due course, and repeatedly, for a long period, if not indefinitely. Allusion has already been made (p. 565) to the causes which contribute to the ultimate death of a sponge of natural growth. Under the very different conditions of repeated subdivision the question of age must still be taken into consideration. On this point it can only be stated that if allowance is made for the probable age of the sponges when cuttings were first made, the total age of the material covered by the present records would not exceed 25 years. This, though likely to be much past the period of increasing growth under natural conditions, is probably still far short of the maximum life limit in similar circumstances.

Regarding this question from another aspect, there can be no doubt that in large sponges which have reached their higher limit of growth, the continued production of larvae amounting in some cases to hundreds of thousands annually must contribute to much impoverishment of the parent. So marked is this wastage in the general body tissues, that at the close of the breeding season it is usually distinctly visible to the eye, in the pitted and impoverished appearance of a section through the living sponge.

With the artificial subdivision of any such sponge, its wider distribution, and the proportionately larger food supply made available to the smaller body, a new factor is introduced, enabling the previously arrested body growth to be resumed. Yet in such conditions the larval production of the fragment is not comparable with that of a young sponge of equal or greater volume, which for some 2 years or so from early maturity is very limited. From the time of planting, the larval production of the fragment is approximately that of its corresponding volume in the original stock and similarly to increase with its own growth.

Whether ultimately this may lead to the death of the parent or not is a question which cannot be solved from the limited records available. In the view of Dr Bidder, whose conclusions on bath sponges are based on past official reports of mine concerning resumption of growth in fragments severed from a fully grown sponge, there is no clear reason to believe that, apart from secondary causes previously referred to (p. 565), any such limitation of life and growth truly and "naturally" exists. With the repeated subdivision of the body of the sponge, in the planting of cuttings, the difficulty of continued self-maintenance beyond the maximum of individual growth is removed, and life should continue indefinitely; nor even should ultimate exhaustion of the parent occur through recurrence of the reproductive process.*

Observations covering about 2000 different sponges, and some 60,000 cuttings derived from them, yield no evidence definitely inconsistent with such a view; that is to say, no distinct example of "senescence" has been observed. From another aspect—and here disregarding partial mortality in the material through external causes, always liable to occur—the total extent of volume increase represented in repeated series of cuttings from a single sponge has, in many experiments, been very far in excess of anything conceivable under conditions of independent growth in that sponge. In the Velvet H. 38, for example (p. 570), an average annual factor of volume increase of 2·3 would in only 8 years lead to the equivalent of a sponge of about 12·8 ft. in average diameter. This would be rather more than four times the average diameter of a very large sponge of the same type, and from the same locality, which I saw several years ago in the warehouse of Messrs Cresswell in London, and probably the largest market sponge on record.

Within the range of the observations, and concerning sponges of a total estimated age not exceeding about 25 years, the recorded evidence seems thus far to support the view that life and growth in sponges of this group has no necessary limit.

I have to express my thanks to the Council of the Marine Biological Association for allowing me the facilities of the Plymouth Laboratory for the preparation of this paper; and to Dr G. P. Bidder for much valuable assistance and advice.

SUMMARY

An account of the chief earlier experiments, from those of Cavolini in 1785 to the close of Moore's experiments in Florida in 1905, is given and the general subject of reconstruction and growth in the sponge cutting is described in detail.

Under favourable conditions loss of volume in the initial stages, following cutting, should be practically negligible, the early steps in repair and recon-

---

* Cf. Bidder (1932). Par. 1: "water voles, female plaice, sea anemones, and the bath sponge do not show senescence". Par. 3: "Pseudo-senescence and pseudo-specific size are often mere consequences of the decrease in ratio of surface to volume as size increases....with increase in size the relative diminution in surface requires higher velocity to feed the sponge, lengths of all channels are increased, and consequent friction becomes more than the flagella can overcome."

struction proceeding without delay after severance of the fragment from the original sponge. As chief among these, the dermal covering required for newly cut surfaces, the closing of most of the exposed apertures of the old canal system, and the retention of one or more of these for future oscula, are accomplished rapidly and, for preliminary purposes, are completed within a very few days.

Pigmentation of new surfaces exposed to the light, though very soon apparent, may require a few weeks for completion. Basal attachment (assuming contact with a fixed basal support) is also soon initiated, but may likewise occupy a few weeks, or several weeks, for purposes of complete natural support. Rotundity—or other prevailing character of form exhibited by the original stock—may be reached in a few months, or in several months, the time varying much with the conditions.

Size of cutting is, for purposes of growth alone, unimportant; the same, or approximately the same, rate of increase occurring in the same sponge under similar conditions, in large fragments or (within limits) in small ones. But, for practical convenience, an optimum size is recommended, equivalent to a sphere of 2·7 in. in average diameter, or a volume of about 10 cu. in.

Shortage of food which probably consists chiefly of bacteria may lead to complete suspension of growth, or even to reduction in volume. But in such cases, even after 2½ years, growth is normally resumed with change to more favourable conditions. Rate of growth amounts, under fair conditions, to an annual factor of volume increase of about 2·0. Under more favourable conditions a factor of 2·5 is frequent, and 3·0, or a higher rate, may be reached, though less likely to be maintained.

Breeding is in no way interrupted in the cutting, but in all respects proceeds normally as in the sponge from which the cutting was derived.

Recutting of the material at any suitable stage of its growth from planting—and so continuing at intervals, through successive series of planted cuttings grown from the same material—is attended with the same results as in the first planted series, except in so far as certain growth variation may occur with change of surroundings.

The maximum growth attainable is limited by that volume—coupled with its form—capable of self-maintenance as an independent unit by the feeding mechanism of the individual sponge. Beyond this point, death may occur through causes associated with that limitation. Whether, under conditions of repeated cutting and redistribution of the stock, life and growth can be prolonged indefinitely or not, is at present uncertain. Within the extent of the numerous recorded observations, there is no evidence inconsistent with this possibility.

REFERENCES

Aristotle, The Works of, 1910. Translated into English under the Editorship of J. A. Smith, M.A. and W. D. Ross, M.A. Vol. iv. *Historia Animalium.* By D'Arcy W. Thompson. Oxford: Clarendon Press.

Bidder, G. P., 1932. Senescence. *British Medical Journal*, September 24.

Cavolini, F., 1785. *Memorie per servire alla Storia de' Polipi Marini*, pp. 265–72. Napoli.

—— 1853. *Memorie postume sceverate dalle schede autografe di...per cura ed a spese di S. D(elle) Chiaie*, pp. 42–51. Benevento.

Drew, G. H., 1914. On the precipitation of calcium carbonate in the sea by marine bacteria, and on the action of denitrifying bacteria in tropical and temperate seas. *Carnegie Institution of Washington, Publication*, No. 182, pp. 7–45.

Marenzeller, E. von, 1878. Die Aufzucht des Badeschwammes aus Theilstücken. *Verhandl. der k. k. zool. bot. Ges. Wien*, Bd. xxviii, pp. 687–94.

Moore, H. F., 1908. A practical method of sponge culture. *Bulletin of the Bureau of Fisheries*, Vol. xxviii. Washington. Bureau of Fisheries, Document No. 669. Issued March 1910.

Rathbun, R., 1887. The sponge fishery and trade. U.S. Comm. Fish and Fisheries. The Fisheries and Fishery Industries of the United States. Sect. V. History and Methods of the Fisheries. Vol. ii, pp. 817–41. Washington.

Schmidt, O., 1862. *Die Spongien des adriatischen Meeres.* Leipzig.

—— 1864. *Supplement der Spongien des adriatischen Meeres. Enthaltend die Histologie und systematische Ergänzungen.* Leipzig.

—— 1878. Brehm's *Thierleben.* Zweite umgearbeitete und vermehrete Auflage. x. Band. Die niederen Thiere. Schwämme. Ordnung 4, pp. 534–5. Leipzig.

Vosmaer, G. C. J., 1887. Porifera. Bronn's *Die Klassen und Ordnungen des Thier-Reichs.* Leipzig und Heidelberg.

PRINTED IN GREAT BRITAIN BY W. LEWIS, M.A., AT THE CAMBRIDGE UNIVERSITY PRESS

MAY 1958
LIBRARY
POFI
FISH & WILDLIFE
SERVICE